Modeling the Effects of Climate Change on Forest Succession in Northern Michigan

by

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I would also like to acknowledge that the University of Michigan Biological Station exists on land once occupied by the Burt Lake Band of Ottawa and Chippewa people. In particular, the Burnout of Burt Lake Village led to their forced displacement in 1900 and the land where that occurred is now Indian Point Reserve. The legacy of that event continues to affect us in the present both socially and ecologically.

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ABSTRACT

Following a well-known successional dynamic in eastern North America, the species composition in many northern Michigan forests is changing as early successional species that colonized after the logging and fires of the early 20th century reach the end of their life spans. What is not well-understood is how changing climate (predicted to be overall warmer and drier by the end of the 21st century) will also influence future species composition. To address this knowledge gap, in this study I modeled forest composition and succession over a regionally representative northern temperate landscape under different climate scenarios. The study site was the University of Michigan Biological Station (4046 ha) in northern Lower Michigan. My objectives were to: 1) develop the needed input data to parameterize, calibrate, and run the LANDIS-II forest landscape model and its PNet succession module at the landscape level, 2) develop three different future climate scenarios for the study region – a static climate scenario, a moderate warming scenario with up to 4 degrees of warming compared to the current climatology, and a high warming scenario with up to 8 degrees of warming compared to the current climatology, and 3) use the parameterized LANDIS-II/PNet models to predict changes in forest successional composition and biomass under the different climate scenarios, and analyze these by regionally-important species and by landform-level ecosystems. Species biomass and response to climate change varied among landform-level ecosystems. Results showed that under all climate scenarios and landforms, the early successional species of birch and aspen decreased. While later successional species like white pine, red maple, sugar maple, beech, balsam fir, oak, and hickory increased in biomass under all climate scenarios, the increase was greater for sugar maple, fir, hickory, hemlock, and oak under the high warming scenario. Red maple increased the most under both the moderate and the high warming scenarios. The overall changes were largest under the high warming scenario. All other species showed mixed or similar increases under all climate scenarios. There was little expansion of species from one landform-level ecosystem type to another within the UMBS area. These results show the influence of potential climate change, and also the continued importance that non-climactic factors such as land-use history and soil fertility have in determining species locations.

1 INTRODUCTION

Secondary succession is the process through which forest communities change over time after a disturbance (Finegan 1984, Horn 1974). This process results from the different responses of the species making up a community to available resources, leading to different rates of growth and establishment as the tree canopy closes (Horn 1974, 1981). Secondary succession in temperate North American upland forest landscapes is often a progression from fast-growing, shade-intolerant pioneer species to shade-tolerant, mid- and late-successional species that can tolerate growing beneath an overstory canopy. In Northern lower Michigan (the location of this study) and the broader upper Great Lakes region, secondary succession has occurred at the landscape scale after disturbances of logging, fire, and the abandonment of agricultural lands (Fahey 2014, Gates 1930, Leahy and Pregitzer 2003, White and Mladenoff 1994, Whitney 1987, Wolter and White 2002). Widespread early successional species include jack pine (*Pinus banksiana* Lamb.), paper birch (*Betula papyrifera* Marshall), yellow birch (*Betula alleghaniensis* Britton), pin cherry (*Prunus pensylvanica* L. f.), bigtooth aspen (*Populus grandidenta* Michx.), and trembling aspen (*Populus tremuloides* Michx.) (Burns and Honkala 1990).

Thus, land-use history and successional stage play large roles in determining species composition of an upper Great Lakes forested landscape at a given point in time. At the same time, climate change may be leading to changes in species range, which may in turn affect community composition on these forested landscapes. Because of a unique land-use history and timing, landscapes of upper Great Lakes forests are presently at the cusp of shifting from early successional aspen and birch forests, to forests dominated by mid-to-late successional species. This poses the question: could climate change lead to different successional pathways and different species gaining dominance? Northern Michigan and my study site at the University of Michigan Biological Station (UMBS) are located within the boreal-temperate transition zone, so if species currently at the northern edge of their range currently present at low densities gain greater dominance, or species at the southern end of their range disappear, this would be a leading indicator. The migration of species northward, either losing boreal species or gaining new southern species, would also be an indicator.

1.1 Background

Prior to European settlement, the major upland forest types of northern Lower Michigan were the white pine-red pine-jack pine association (*Pinus strobus* L., *Pinus resinosa* Aiton, *Pinus* *banksiana* Lamb.), and the eastern hemlock-sugar maple-American beech association (also known as the northern hardwoods association; *Tsuga canadensis* (L.) Carrière, *Acer saccharum* Marshall, *Fagus grandifolia* Ehrh.). Oaks, including northern red oak (*Quercus rubra* L.) were also found in association with either the pines or other hardwoods. Deforestation and burning during the logging boom of the late 19th and early 20th centuries led to a large change in species composition, with early successional species of paper birch, trembling aspen, and bigtooth aspen colonizing the burned-over lands and coming to dominate the new overstory (Barnes 2010, Fahey 2014, Gates 1930, Hanberry et al. 2012, Leahy and Pregitzer 2013, Palik and Pregitzer 1992, Paulson et al. 2016, Whitney 1987). Today, these early successional species are reaching the end of their natural lifespans, and later successional species, including many but not all of those present on the landscape prior to the logging era, are in part replacing them (Bergen and Dronova 2007, Fahey 2014, Gough et al. 2010).

In the region of my study, the successional pathway that forests undergo is in part controlled by geological landform. Tree species differ in how well they can use available resources, compete against other trees, and withstand low resources. Geological landforms vary in texture, and consequently soil resource availability. The variance in soil resources among landforms leads to different species outcompeting others, and therefore to different communities (Kobe 2006, Schreeg et al. 2005, Zak et al. 1986). Thus, different landforms support different species (Host and Pregitzer 1987, Ricart et al. 2020) and produce biomass at different rates (Nave et al. 2017). Within northern Lower Michigan, ice contact landforms and moraine landforms tend to regenerate to the northern hardwoods association and have the highest rates of biomass production, whereas well-drained outwash sites tend to regenerate to the pine association, or an oak-pine association, and have lower biomass production rates (Bergen and Dronova 2007, Host et al. 1987, Host et al. 1988, Nave et al. 2017).

At the same time that late-successional species are succeeding into the overstory in this region, climate change is occurring. Under several published climate warming scenarios, northern Michigan is predicted to become much warmer throughout the year, with increases in winter precipitation and intensified precipitation events and decreases in summer precipitation (d'Orgeville et al. 2014, Hayhoe et al. 2010, Kling et al. 2003, Zhang et al. 2018, Zhang et al. 2020). These changes could, theoretically, lead to different species gaining a competitive edge, and the dominance or creation of novel species associations.

The resilience of each individual tree species to climatic extremes such as drought or cold is a major factor in determining species range (Box 1995, Clark et al. 2016, Parker 1963, Stephenson 1990). A changing climate could give species an advantage where there was none before. Thus, changes in temperature or water availability can cause changes in species composition in a particular site, and on a broader scale, shifts in a species' range (Chuine and Beaubien 2001, Parker 1963, Stephenson 1990). The temperate-boreal transition zone, which has species from both ecosystems, is thought to be highly sensitive to change in climate (Goldblum and Rigg 2010, Pastor and Post 1988), and previous studies found that the upper Great Lakes region was one of the US regions most sensitive to changes in temperature and precipitation (Clark et al. 2014, Motew and Kucharik 2013, Zhu et al. 2012). Seedling recruitment is increasing in northern forests that are growing warmer and wetter (Sharma et al. 2022).

Climate envelope models use the climate of species' current range to predict its potential habitat under climate change (Hijmans and Graham 2006). For years, models of the climate-envelope type have predicted large latitudinal shifts in tree ranges under high warming scenarios, to the north and east (Iverson and Prasad 1998, Iverson et al. 2008, Iverson et al. 2019) and reductions in habitat size of many important northern Michigan species (McKenney et al. 2007). These models have predicted the extirpation of suitable habitat within the upper Great Lakes region for species such as sugar maple, balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), bigtooth aspen, trembling aspen, paper birch, and red pine (Iverson et al. 2008). Meanwhile, the ranges of oak and hickory are predicted to move north and become an important part of the forest ecosystem (Overpeck 1991, Iverson et al. 2008). Although they are not extirpated in the northern United States, beech and red maple are predicted to decrease in abundance in the Upper Great Lakes region, and beech's population center moves upwards along an altitudinal gradient and slightly south to the Appalachian Mountains. (Iverson and Prasad 2002, Iverson et al. 2008). Climate-envelope models, however, have some notable drawbacks, such as not accounting for species interactions and competition (Ibáñez et al. 2006).

Implementations of successional-based landscape models, such as LANDIS-II, that model forest dynamics including competition for light and water, have also predicted shifts in range and species composition (Iverson et al. 2017, Scheller and Mladenoff 2005, Duveneck et al. 2014). However, many of these previous LANDIS-II studies, while considering succession and disturbance, largely make use of imputation of very sparsely distributed data over large landscapes, increasing uncertainty and decreasing ability to relate responses to landscape-level ecosystem properties.

Due to the long lifespan of trees, it will be years before any major shifts in species composition and range due to climate change or succession are documented. Experimental data on climate change looks mainly at the effect climate change has on tree recruitment, seedlings, and saplings, while most studies of forest succession only compare the past to the present. At the same time, climate change is affecting species regeneration, leading to changing successional patterns different from the past. (Leithead et al. 2010, Sharma et al. 2022). To look into the future, we need to model both succession and climate change.

Although this study of present and future forest composition and succession looks at climate and succession together on the landscape, similar to many previous LANDIS-II studies, this study site is smaller and very well understood, so there is a larger pool of existing data to draw from. Also, this study site contains a range of landscape types that are representative of many parts of the upper Great Lakes region, and so results can be extensible to broader landscapes.

1.2 Goal and Objectives

My study is therefore driven by several research questions: how will forests in Northern Michigan (and at UMBS specifically) develop over the next 100 years? will climate change influence successional species composition? Are some species affected more than others? how will this vary by landform-level ecosystems? These questions suggest that a modeling approach incorporating successional processes over landscapes and tree physiological response to climate would be useful. Thus, the primary goal of my study is to model the process of forest ecological succession over a complex and representative landscape using the LANDIS-II/PnET forest landscape model and under three different climate scenarios. The specific objectives are to:

1. Develop the needed input data to parameterize, calibrate, and run LANDIS-II and the PNet succession module at the landscape level.
2. Develop three different climate scenarios for the study region – a static climate scenario, a moderate warming scenario, and a high warming scenario.
3. Use the parameterized LANDIS-II/PNet model to predict changes in forest successional composition and biomass under the different climate scenarios and analyze these by regionally-important species and by landform-level ecosystems.

2 STUDY SITE

The University of Michigan Biological Station (UMBS) occupies 42.5 sq km in northern Lower Michigan, near Pellston, MI, at 45.6 N, 84.7 W (Figure 1). Over the past thirty years, the mean annual precipitation was 871.01 mm, the mean January temperature was -7.4° C, and the mean July temperature was 19.6° C (PRISM 2023). Ecologically, UMBS is situated on the transition zone between the boreal and temperate biomes (Barnes 2010, Goldblum and Rigg 2010).

There is significant variation in the physical and ecological factors of UMBS, due in part to the variety of geological landforms present at the site. The geological landforms and soils at UMBS are the result of the most recent glaciation acting upon the landscape and they affect nutrient availability, drainage, and soil quality. Therefore, geological landform also plays a large role in determining species composition, successional pathway, and biomass levels (Bergen and Dronova 2007, Host et al. 1987, Host et al. 1988, Nave et al. 2017, Pearsall 1995, Zak et al. 1986). This variety makes UMBS a good location to study ecosystems found across the Upper Great Lakes.

Pearsall (1995) identified nine major landforms present over the UMBS property. The interlobate moraine landform occupies much of the southwest of the property. It has the loamiest soil and the highest rates of biomass production (Nave et al. 2017). On this landform, hemlock and northern hardwoods dominated the land cover before European settlement, and the region is currently transitioning from bigtooth aspen to northern hardwoods (Barnes 2010, Bergen and Dronova 2007). To its north, there is a shallow ponded depression formed by melting ice eroding the interlobate moraine.

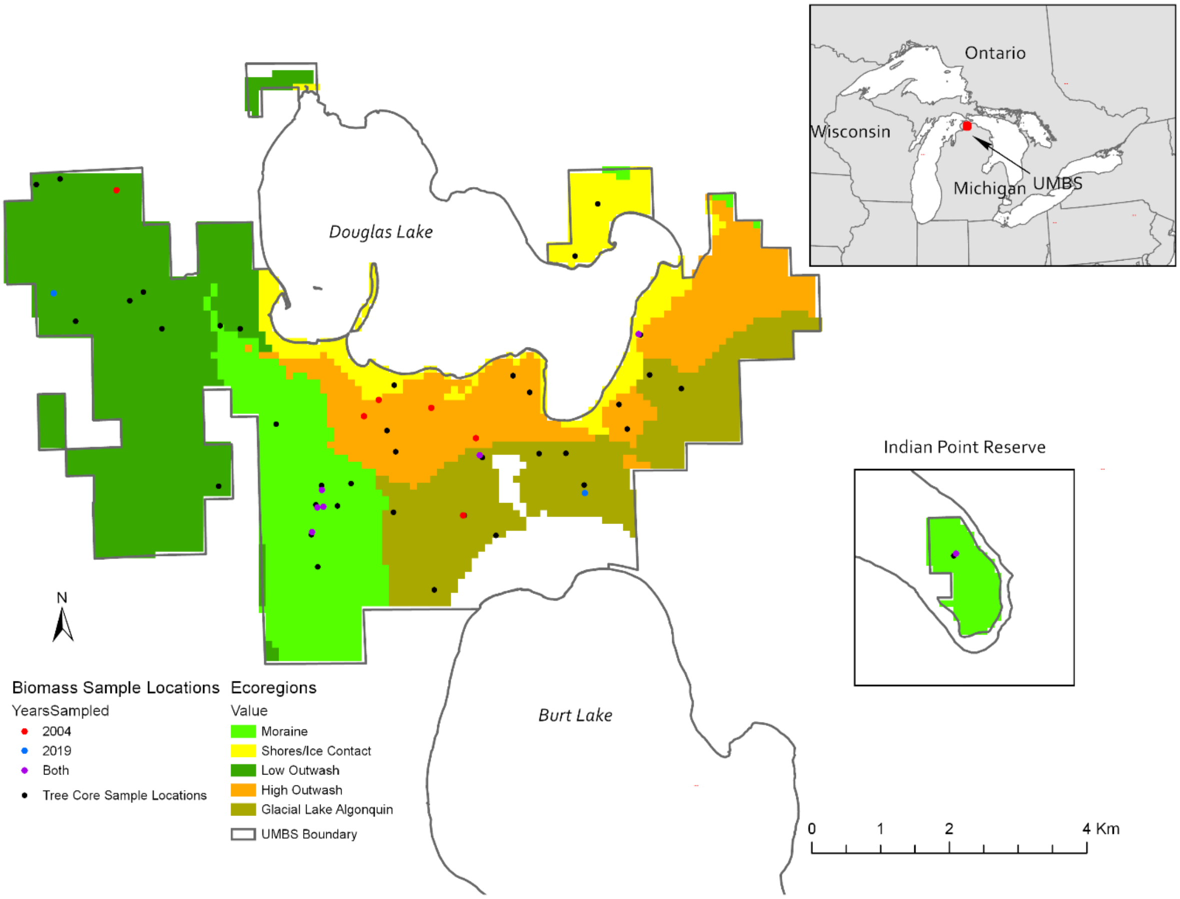


Figure 1. Shown are the LANDIS-II ecoregions derived from the major landforms of UMBS (main map, Pearsall 1995) plus locations of study field and tree-core plots (circles). Also shown is the location of the UMBS within the upper Great Lakes region (top right inset) and Indian Point Reserve, formerly known as Colonial Point, located south of the main UMBS property by Burt Lake (bottom right inset).

The low outwash landform is located in the western part of the property and is part of the Pellston Plain, which occupies a large area. The soils of most of the low outwash are sandy, with hardpan sometimes present, but to the north there is a small band of loamy sand (Pearsall 1995). The cover type, historically and today, is largely pine, although there are still aspen stands present. The water table in this region is very high and the climate is more prone to extreme temperatures, so in moister (but still upland) areas, species like white spruce, balsam fir, and trembling aspen are found with greater frequency.

The High Outwash and Glacial Lake Algonquin landforms are largely located in between Douglas Lake and Burt Lake. Both landforms are both very sandy and well drained, although Glacial Lake Algonquin has slightly richer soils. The pre-European settlement land cover consisted of white pine-oak associations (Barnes 2010). Currently, the overstory consists of bigtooth aspen with a pine understory, with remnant oaks scattered throughout. There are more hardwoods located in the High Outwash closer to Douglas Lake.

The shores and lake terraces surrounding Douglas Lake are also identified as a landform. The is also a small section of ice-contact terrain located primarily in a disjunct section north of Douglas Lake. The soils for both these regions are sandy, but have higher fertility and support a variety of hardwood and conifer species, including some that are rare within the greater UMBS landscape, such as old-growth white ash (*Fraxinus americana* L.) , American basswood (*Tilia americana* L.), and young hemlock.

There are also two wetland landforms. Glacial Lake Nippissing is located immediately to the north of Burt Lake, and is dominated by Reese’s swamp, a wetland area dominated by spruce and fir. Little Carp River Gorge is located in the high outwash, but his low-lying river gorge supports a much wider range of species than its surroundings. Because processes acting within true wetland areas are so different from the more widespread uplands, wetland ecosystems are excluded from the study.

Like much of the upper Great Lakes region, the land that would become UMBS, with the exception of Indian Point Reserve (Figure 1), was logged intensively starting in the 1840s, removing much of the old growth red pine and white pine. The logging was then followed by repetitive fires through the early 1900s. The dominant upland forest species then shifted from white pine-oak associations and eastern hemlock-northern hardwood associations to stands consisting of early successional species of trembling and bigtooth aspen and paper birch (Barnes 2010, Bergen and Dronova 2007, Fahey 2014, Gates 1930, Gough et al. 2010, Kilburn 1957, Nave et al. 2017, Palik and Pregitzer 1992, Whitney 1987). As the landscape regenerated, fire suppression led to fire intolerant species expanding their range. Red maple, previously limited to swampy wetland areas, moved into more upland ecosystems as part of the process of mesophication (Abrams 1998, Barnes 2010). In the 1930s, when UMBS was used as a field site for the then-School of Forestry, several pine plantations were planted in the high outwash and Glacial Lake Algonquin landforms. Remnants of these plantations survive to this day. Of note is Indian Point Reserve, a disjunct part of UMBS located next to Burt Lake, which was not logged and contains the only old-growth forest at UMBS. This area was the traditional location of the Burt Lake Band of Ottawa and Chippewa Indians until the Burt Lake Burnout led to their forced removal, and the impact of their farming practices affects the species composition to this day (Albert and Minc 1987).

3 METHODS

3.1 LANDIS-II Overview

LANDIS-II is a forest landscape model first described in Scheller & Mladenoff (2004). It models forest succession on a spatially explicit raster field and includes several disturbance extensions. I chose this model environment because of the capability to model complex spatial processes, its history of being a well-tested model, and because it has been parameterized (for other sites) in the upper Great Lakes region. Available for integrations with the LANDIS-II core model, there are multiple succession extensions. I chose the PNET-II succession extension (de Bruijn et al. 2014, Radtke et al. 2001) because it can model the effect of climate change on tree growth in a mechanistic fashion. This succession extension outputs biomass data and age cohort data for each species for each grid cell at a user-defined time step. No disturbance extensions were included at this time.

The required input for the LANDIS-II base model includes a map of ‘ecoregions’, areas with similar ecological conditions, their associated ecoregion parameters, and a site initialization map of ‘initial communities’ containing species and age information for each site (i.e. raster cell). The PNET-II succession extension requires life history and physiological data for each species. The major landform-level ecosystems and their boundaries identified by Pearsall (1995), with some modifications, were used as ecoregions in this model run. The site initialization data was derived from existing remote-sensing datasets and field data collected for this project. Parameters for species life history and the ecoregions were derived from existing UMBS datasets or the regional literature. Climate data was derived from the National Oceanic and Atmospheric Administration's (NOAA) Climate Divisional Database (Vose et al. 2014) and the United States Geological Survey (USGS) Geodata Portal (Blodgett et al. 2011, USGS 2018). The two emission scenarios chosen were the were the Representative Concentration Pathway (RCP) 4.5 and RCP 8.5. RCP 4. 5 stabilizes radiative forcing to 4.5 W/m^2 by 2100 and represents a medium-low greenhouse gas emissions scenario. RCP 8.5 stabilizes radiative forcing to 8.5 w/m^2 by 2100 and represents a high emissions scenario (Collins et al. 2013). These two scenarios were identified as the highest priority scenarios in the CMIP5 model runs (Taylor et al. 2012). Additional detail on all inputs is given below.

3.2 Model Inputs: Ecoregions

LANDIS-II requires an input raster map of geologically and climactically distinct model ecoregions. Due to the relatively small study area, climate did not significantly differ between different ecoregions, so geological data only was used to create the ecoregions. These data were based on the major landform-level ecosystems (hereafter landform) that had been delineated as vector polygons by Pearsall (1995) and discussed above, due to the abundance of previous research showing distinct ecological communities on each type. The present study looked at the upland regions of UMBS only, so two relatively localized landforms identified by Pearsall were excluded due to being more than 50% wetland (Glacial Lake Nipissing and Little Carp River Gorge). The remaining major landforms are the Moraine, Glacial Lake Algonquin, Low Outwash, High Outwash, Shores and Lake Terraces, Ice Contact, and Shallow Ponded Depression. For the present project, some minor changes were made to the original spatial delineation of the landforms based on comparison with the Soil Survey Geographic Database (SSURGO) dataset for this region and the observation of different plant communities on those specific sections (NRCS 2019).

The Moraine, the Shallow Ponded Depression, and a portion of the Low Outwash dominated by northern hardwoods were grouped together due to similarities in soil type. The soils of these landforms were primarily sand; grouped together these will hereafter be referred to as the Moraine ecoregion. The final two landforms, Ice Contact and Shores and Lake terraces were grouped together due to their small area, sandy soils, similar species composition, and close proximity to Douglas Lake. The Glacial Lake Algonquin and High Outwash landforms remained unchanged. The modified major landform vector polygon data were converted into a raster with 100 m x 100 m spatial resolution and this formed the ecoregion inputs for the modeling (Appendix Figure A).

3.3 Model Inputs: Species-Age Cohorts at UMBS

The initial communities input map required by LANDIS-II consists of unique species-age cohorts that separate the age structure of each species in that community at a modeling ‘site’ (i.e. an individual 100 m resolution raster cell) into user-determined 10-year age range bins. This map initializes the model with the current land cover and species-age composition during model spin-up. We developed new initial community species-age cohorts inputs for this study through field plot sampling and tree cores collected summers 2018 and 2019 (described below). Community structure and tree cores were collected over the UMBS landscape using a stratified sampling plan based on the spatial intersection between major landforms and remotely-sensed forest cover type data (Appendix A), with number of plots allocated proportional to the type on the landscape.

Locations for sampling field plots were selected using the spatial intersection between major landform and remotely-sensed forest cover type because there is variation in forest communities within landforms. Using the combination of landform and cover type allowed me to sample the species differences in deciduous and coniferous forests within the same landforms and across them. Cover type information for stratification was derived from the Landsat-derived cover type and forest successional pathway map of Bergen and Dronova (2007) because this spatial dataset considers understory composition as well as currently dominant overstory. This raster data was resampled from 30 m x 30 m resolution to 100 m x 100 m (1 ha), the size of the planned LANDIS-II model raster cell, using the nearest neighbor method. The LANDIS-II ecoregion map using the modified Pearsall (1995) landforms was used as the source for landform information. There were five unique ecoregions as previously described (Appendix A) and nine unique cover types (Appendix B). However, not all cover types were present on all ecoregions. The cover type and major landform rasters were combined in ArcGIS Pro 2.3.2 (ESRI 2019) using the “Combine” function so that a unique value was generated for each combination of values. Initially, there were 54 unique combinations, so unique cover type/landform combinations with fewer than 40 cells were grouped together with the most ecologically similar larger land-cover type within the same ecoregion.

This intersection of the ecoregion raster and cover type raster was used as the initial basis for the GIS layer I used as the initial communities raster. However, Indian Point Reserve lands, former conifer plantations, and areas where trees had been thinned, were separated out from the rest of the landscape due to different land-use histories. A few other cover types were grouped together due to the similarities between the age distribution and species composition present at those sites (Appendix A). The resulting map of the modified intersection of ecoregion and cover type formed the raster grid for which species-age cohort information would be attached for each cell. Each cell in turn formed the ‘site’ on which the LANDIS-II/PNET models would be run.

To determine the number of species-age cohort field sample plots per unique cover type/ecoregion combination for a proportional allocation, a Natural Breaks (Jenks) algorithm was used to split the cover type/ecoregion combinations into groups based on area, with three sample plots allocated to those in the greatest area range, two plots for those in the middle area range, and one plot at the lowest area range. Thirty-six plots were selected for sampling using this method in 2018. In 2019, five more plots were sampled to better include the areas with unique land-use histories, or to fill in gaps where the original plots were determined to not be as representative of its type due to history as originally expected. Specific plot locations were chosen primarily for their representativeness, and secondarily for access feasibility and for proximity to existing research plots at UMBS through combining spatial data in ArcGIS. Due to later reclassification of some plots and time constraints on sampling, the number of plots sampled per unique cover type/landform combination varied to a minor extent from the initial proportional allocation (Appendix A).

We used a circular plot sampling methodology for the field measurement of species-age cohort data. A circular plot with a 10-m radius was set at or near a planned plot location, with a subplot of 3-m radius located 5 meters east of the main plot center. The plot locations were recorded using ArcGIS Collector (ESRI 2019) and the GPS (Global Positioning System) of an iPad and iPhone. Species and diameter at breast height (dbh) were recorded for every tree > 9 cm dbh in the main plot and noted on paper forms. In addition, a tree core was taken using a 14’’ Haglöf tree corer for one tree of every species for each 10-cm size dbh increment, starting with a 9-20 cm range for the first, size class, then 20-30 cm, etc. These cores were later analyzed for age (described in a subsequent section below). Sampling was limited to the above N of and size of plots as tree-coring (especially for large hardwood trees) and subsequent core interpretation is very intensive. Thus in a few cases, where previous data indicated the frequent presence of a tree species of a given dbh range in the general vicinity but not present in the plot, a tree core was taken outside of the plot to ensure that all age cohorts could be represented in the model even if a plot did not turn out to be more fully representative.

Trees <9 cm were measured in the subplot. If they were greater than dbh height, then dbh was measured. A tree core was only taken if the tree had a dbh >4 cm and looked physically sound. If a viable tree core was not an option, then the age of conifer seedlings and saplings was determined directly in the field by node counting. If the sapling was too small to core and the age could not be determined by node counting, or if there were seedlings, their presence was noted for inclusion in the youngest age class.

Tree cores were taken back to the lab at the UMBS station. To determine age from the tree cores, I mounted cores on wood blocks and sanded them using progressively finer sandpaper, and then scanned them. The scanned images were uploaded and the number of rings counted using CooRecorder (Cybis Electronik 2010). If the tree core was broken or incomplete, the age was estimated using CooRecorder's software and the radius of the tree. If no age could be read from a core for a tree in a given plot, the age was estimated from a core of the same species and size class in a nearby plot. To ensure the accuracy of the age estimates, I cross-dated a subsample of the tree cores using CDendro (Cybis Electonik 2010). Cross dating ensures that the calendar for each year of growth is identified without false or missing rings, enabling the accurate identification of climate trends from growth rings. (Fritts 2012).

3.4 Model Inputs: Biomass

Live, aboveground tree biomass was sampled at eight field plots/stands. The biomass data in Bergen and Dronova (2007), sampled in 2004, was used as a starting point. Six of those plots/stands were resampled in 2018 and 2019, and another two representing community types that were not sampled in the original dataset. A 100 m transect was laid out with three 60 m plus a random offset of 1-10 m transects laid 30 m apart. Two circular plots were sampled along each of the 60 m transects every 30 m, for a total of 6 plots. Each plot was 100 m^2 with a radius of 5.64 m. Within each plot, there were two subplots 16 m^2 each with a radius of 2.82 m. Aboveground overstory data was collected by taking the dbh of every live stem ≥9 cm dbh in the large plots. Aboveground understory data was collected by taking the dbh of every live stem ≥3 cm dbh and <9 cm dbh in the two subplots. Then, the biomass for each stem was calculated using species-specific allometric equations for the Great Lakes area (Perala and Alban 1994, Ter-Mikaelian and Korzukhin 1997). The Mg/ha of aboveground biomass were calculated based on the plot size and the total aboveground biomass for each plot.

3.5 Model Inputs: Initial Communities

Within LANDIS-II, each cell in a 100 x 100 m raster is considered a modeling "site". For the LANDIS-II initial communities raster, each cell has a value, and that value refers to a particular community type formed from a set of species-age cohorts. Each set of species-age cohorts was created from the above field and GIS work by grouping each species found on each cover type/landform combination in the field data into 10-year age bins, creating different community types on the landscape. In LANDIS-II, initial communities and ecoregions are independent of one another, but because of how the field sampling was stratified by ecoregion, the community types in this model are generally unique to each ecoregion, with a few exceptions (Appendix A). The resulting community types were then listed in a text file for input to LANDIS-II. The input maps used as the LANDIS-II initial communities raster were based on the simplified cover type/ecoregion combinations (Appendix A) and used the same 100 x 100 m resolution.

Two versions of these input maps were created for modeling (Figure 2). The first version maintained a constant species composition across all cells of a given community type. Meaning that in the initial communities raster, the species-age cohort data from all field-sampled plots combined located on that community type were assigned as present on all raster sites (cells) with the value associated with that community. The second version used the Random Landscape Tool (Fox 2017) to create a random distribution of species and age based on individual field plots data. These were assigned (randomly) among cells of each unique cover type/landform combination. This means that each raster cell within each community type was assigned the species and age data associated with a specific field plot from that community type, rather than aggregated species-age data from all plots on that community type. A rationale for the latter is that it is possible that using individual rather than grouped plot data to represent each site more closely represents the actual spatially-varying distribution of species across the landscape. For example, a rare species found only in one plot would be represented on all raster sites using the first version, leading to an overestimation of its biomass. However, the second version still doesn’t represent the landscape perfectly, as each field plot in a community had an equal chance to be assigned to each cell in that community type in the raster, regardless of its frequency in the actual landscape. Also, the cells containing the actual sampled field plots may not be assigned the correct plot, because the plot assigned to each raster cell is random.

A further two input maps were created based on the uniform input map and the random input map. These input maps were created to test the range extensibility of a more southern species not currently found at UMBS, shagbark hickory (*Carya ovata* (Mill.) K. Koch), and its possible success in northern Michigan under climate change either through natural migration or through human assisted transplantation. These two input maps were identical to the previous two, but they included hickory in the youngest age class as an understory in the ‘Thinned Hardwood’/ ‘Plot 18’ community type. This community type was chosen because the thinning could allow for more successful establishment of hickory.

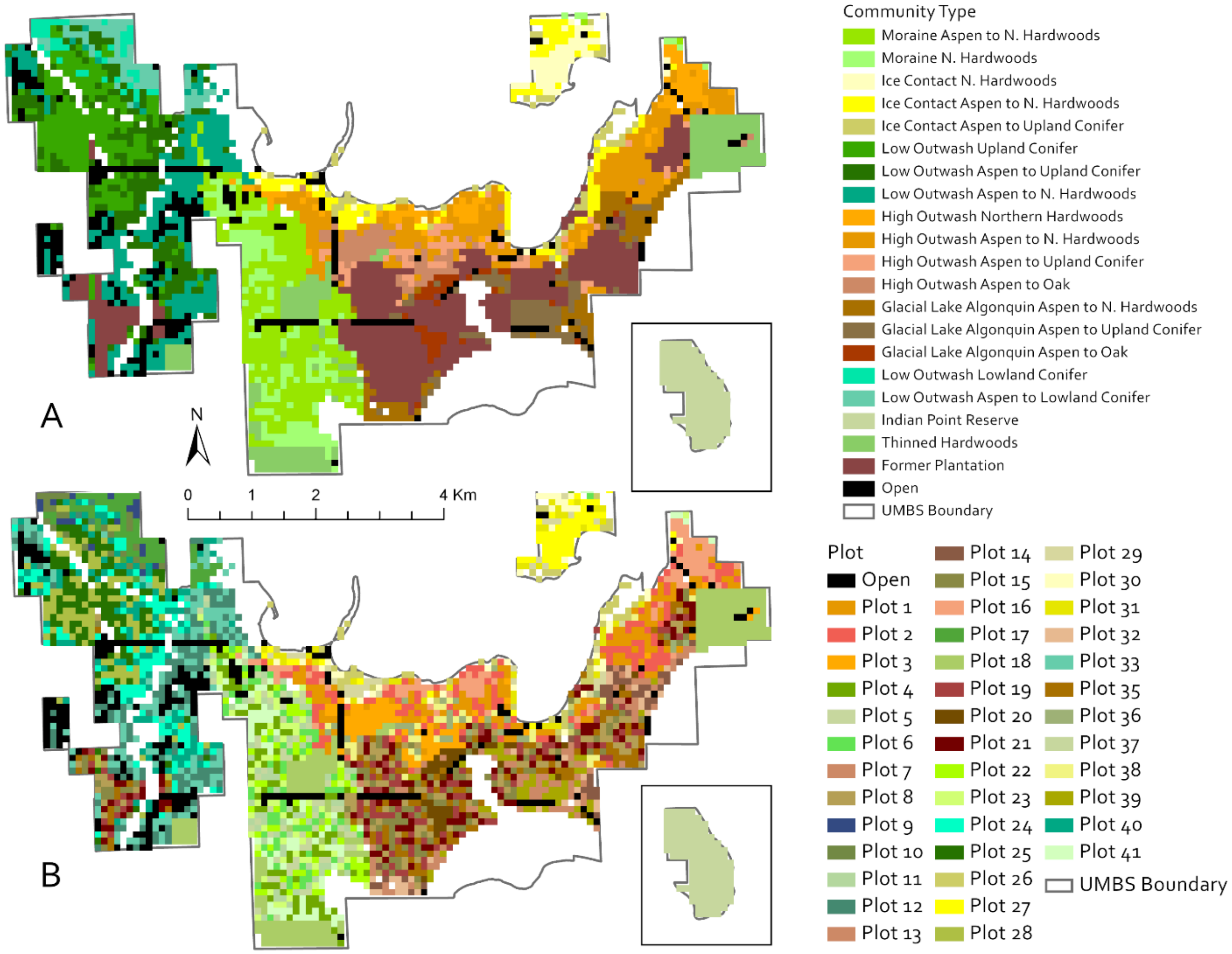


Figure 2. Shown are the two alternative finalized initial communities rasters (a, b) used as input to the LANDIS-II/PNET model. Initial community raster A combined the field data from sampled plots to create community types. Initial community raster B used the Random Landscape Tool to populate each cell or each community type in initial community raster A with the data of a specific field plot, leading to more heterogeneity.

3.6 Model Inputs: Ecoregion and Species Parameterization

LANDIS-II requires additional parameterization for the physical properties of site ecoregions and for site main species physiology and life history. The ecoregion parameters were largely derived from Pearsall (1995). The rooting depth for each ecoregion was calculated using a weighted mean for each ecosystem type identified by Pearsall (1995). The maximum soil depth allowable by the LANDIS-II program was less than the value calculated for three of the ecoregions, so the maximum soil depth value of 1000 mm was used. Soil texture parameters were initially identified using the SSURGO data and further calibrated (NRCS 2019). Both the soil texture and fraction of water drainage parameters were used to modulate the biomass output of the model, rather than empirical values. This was the best way to manage fertility, as the PNET-LANDIS-II extension does not have a nitrogen value the user can change. The fraction of water drainage was determined qualitatively based on the relative drainage and fertility of each ecoregion, based on the landform descriptions in Pearsall (1995), with the well-drained High Outwash having the highest value. I compared the aboveground biomass estimate per ecoregion output by the model to the aboveground biomass values collected at eight field sites and adjusted the fraction of water drainage accordingly. All other ecoregion parameters used the default LANDIS-II values.

For species parameterization, the fourteen most common overstory species within our field plots were selected for inclusion in the model. These in turn included virtually all upland UMBS species. PNET-II requires species life history and physiological data, which was obtained from existing UMBS field-derived datasets or the literature. Values from previous field research at UMBS were prioritized when available. If there were no values from UMBS, we used a value from elsewhere in the upper Great Lakes region, and finally elsewhere in the eastern USA. A fifteenth species, shagbark hickory, not currently measured and rarely found within the region but with possible range extensibility due to its location in southern Michigan, was also included. The general LANDIS-II parameters that control non-species-specific properties used the default values obtained from Scheller and Mladenoff (2005); those from de Bruijn et al. (2014) were used for PNET-II.

3.7 Climate Scenarios

Creating the climate scenarios required synthesis of several sources of data. Climate input data required by the LANDIS-II model includes mean minimum surface air temperature, mean maximum surface air temperature, mean precipitation rate, carbon dioxide concentration (CO_2), and photosynthetically active radiation (PAR) for each month and year.

PAR data from the FASET (Forest Accelerated Succession ExperimenT) tower at UMBS (Bigelow et al. 1998, CSU 2019) was available from 16 July 2003 to 2 Aug 2009 at a temporal resolution of three minutes and the monthly mean PAR (photosynthetically active radiation) during daylight was computed using an R program in RStudio (v4.1.2; R Core Team 2019, v 2022.12.0-353; RStudio Team 2023). I assumed that PAR data would not change significantly under climate change and used the same values for all model runs, although acknowledging that changes in future cloudiness could influence surface PAR.

Maximum air temperature, minimum air temperature, and precipitation were obtained from two separate sources. Historical county-level data from 1895 to 13 May 2020 were downloaded from NOAA's National Climate Division Database (Vose et al. 2014). UMBS straddles Emmet and Cheboygan counties, so data from both counties were averaged together. This dataset does not have data before 1895, whereas the model spin-up starts in 1837. To create historical climate data for the model to use before 1895, I estimated a monthly climatology using the mean of data from 1895 to 1925. While the dataset does not extend as far back as 1850, the beginning of the industrial era as determined by CMIP5 and thus the start of human-induced climate change, the effect of climate change at this early point is minimal.

Future climate data came from seven Coupled Model Intercomparison Project Phase 5 (CMIP5) models (Taylor et al. 2012). Daily minimum surface air temperature, daily maximum surface air temperature, and daily precipitation rate were downloaded (Blodgett et al. 2011, USGS 2018). The models used were the access1-0, canesm2, cesm1-cam5, gfdl-esm2g, hadgem2-es, mpi-esm-mr, and miroc5 models, and the time covered January 1, 1950 to December 31, 2099. To allow evaluation of regional and more local-scale trends, the data were statistically downscaled to a 1/16° (approximately 7 km) grid resolution using the Localized Constructed Analogs (LOCA) method. This method successfully captures extreme temperatures and precipitation while preserving spatial variability, compared to other statistical downscaling techniques (Pierce et al. 2014). Multi-model ensembles are often more accurate than a single model's forecast due to the effects of model uncertainty and bias (Tebaldi and Knutti 2007). To analyze the precipitation, minimum temperature, and maximum temperature data, monthly means were calculated for each emissions scenario based on the daily projections for each variable in each model. Due to the small study area, these means were also spatially averaged by me. Because I was using historical data and data from the CMIP5 models, I had to bias-correct the model data to prevent bias from affecting the data. Climate change models often have a high degree of inaccuracy when compared to local historical records because of the coarse resolution, bias, and generalizations implicit in the models (Navarro-Racines et al. 2020, Ramirez-Villegas et al. 2013). I used the delta-change bias correction method for spatially downscaling data to correct this and make my historical data and my future climate model data comparable. The delta-change bias correction method calculates a reference climatology for both the model and the local data, and adds the difference between the model climatology and the model data for each data point to the local data (Maraun 2016). The reference period I used for both climatologies was from 1989-2019.

Historical CO_2 levels were obtained from two sources. Data from 1850-2005 came from various sources that have been compiled by the National Aeronautics and Space Administration (NASA) (Hansen et al. 2005, NASA-GISS 2005). As this compilation only extended to 2005, CO_2 concentrations from 2006-2019 were downloaded from NOAA (Tans and Keeling 2020) and added to the data. I assumed that the 1850 value for CO_2 concentrations was the same as the CO_2 concentration pre-1850. I downloaded modeled future CO_2 separately from the CMIP5 database, as it is a global variable that did not vary in space in the models or need downscaling. Four of the seven models—canesm2, gfdl-esm2g, miroc5, and mpi-esm-mr—were Earth system models and modeled carbon dioxide levels dynamically. The three remaining models used the CMIP5 prescribed carbon dioxide levels. I calculated a weighted mean using the CMIP5 CO_2 values and the CO_2 values from the Earth system models to use in LANDIS-II.

Next, I developed the three climate scenarios based on high, medium, and no climate change. All three scenarios used the monthly PAR data and the historical data from 1895-2019. I used the climatology from 1895-1925 to represent pre-1895 climate, again, for all three scenarios. The scenario with no climate change beyond 2019, hereafter referred to as the base climate scenario, used the historical data from 1989-2019 to simulate future climate. A monthly climatology using the mean data from 1989 to 2019 was created to extend the base climate scenario out to 2100. To create the base climate scenario, I used the climatology from 1895-1925 to represent pre-1895 climate, the historical data from 1895-2019, and the climatology from 1989-2019 to represent a stable future climate. CO_2 levels were extended using the first and last values respectively. To create the RCP 4.5 and RCP 8.5 emissions scenarios, I used the same historical data from 1830-2019, and the bias-corrected LOCA data from 2019-2100 for each respective scenario. The statistical software R in Rstudio was used for all calculations (v4.1.2; R Core Team 2019, v 2022.12.0-353; RStudio Team 2023). See the table below for the full list of data sources.

Table 1: The data sources used for constructing the climate scenarios

Scenario	Tmin, Tmax, Prec	CO2	PAR
Base	1830-1894: computed NOAA climatology 1895-2019: NOAA 2019-2100: computed NOAA climatology	1830-1850: 1850 value 1850-2005: CMIP5 historical values 2006-2019: NOAA 2019-2100: 2019 value	UMBS
RCP4.5	1830-1894: computed NOAA climatology 1895-2019: NOAA 2019-2100: computed CMIP5 mean	1830-1850: 1850 value 1850-2005: CMIP5 historical values 2006-2019: NOAA 2019-2100: CMIP5	UMBS
RCP8.5	1830-1894: computed NOAA climatology 1895-2019: NOAA 2019-2100: computed CMIP5 mean	1830-1850: 1850 value 1850-2005: CMIP5 historical values 2006-2019: NOAA 2019-2100: CMIP5	UMBS

3.8 Model Calibration

To calibrate the LANDIS-II model, I compared estimates from the model to values at specific field sites where I had collected biomass data and published data from UMBS (Dronova et al. 2011). First, the ecoregion parameters were adjusted so that the total biomass output from the model for each ecoregion was similar to the total biomass per plot and per landform from the field data but within understood ecological ranges for parameters. Some of the soil parameters were changed from the initial values calculated from the SSURGO data to ensure the overall accuracy of the model. The initial model test runs showed little difference in biomass between ecoregions, even where large differences in aboveground biomass existed between low-fertility ecoregions like the High Outwash and high-fertility ecoregions like the Moraine. The initial parameter values overestimated the amount of expected biomass in the High Outwash and Low Outwash and under-estimated the amount of expected biomass in the Ice Contact/Shoreline and the Moraine. Therefore, I decreased the percent organic matter for the High Outwash and the Low Outwash and increased the amount of sand in the High Outwash to decrease productivity from their empirical values based on the SSURGO data. I changed the soil type from SSURGO values to silty clay (a default parameterization) for the Moraine and Ice-Contact to increase productivity to levels similar to those seen in Dronova et al. (2011) and my field data. This reflects a limitation in the model. Because there is no soil fertility parameter, controlling the biomass output of an ecoregion must be done through limiting water availability, which is controlled by the soil parameters. The soils of UMBS are mostly sandy in every ecoregion, and the differences in soil type between ecoregions were too small to reflect the range of biomass values present across ecoregions when I used the values in the SSURGO dataset without parametrization.

Second, I adjusted the species parameters so that the model output them in similar proportions to the field data. The initial model underestimated the amount of bigtooth aspen and red maple, and overestimated the amount of beech. I increased the maximum age of aspen to 120. While literature on the subject indicated that bigtooth aspen rarely exceed 100 years (Burns and Honkala 1990), trees older than that were not uncommon at the UMBS study site. I increased the percent foliar nitrogen of red maple and bigtooth aspen, to better reflect their competitive ability in the landscape, and decreased the foliar nitrogen of beech. In addition, the model overestimated the amount of white pine biomass in the Low Outwash. I removed the oldest cohorts (100+ years) from the initialization file. While there are large white pine present on the landscape, they are all remnants from the previous logging era and are not representative of the broader landscape (Gates 1930, Pearsall 1995).

Once parameters were adjusted and finalized (Table 3), the LANDISII model versions were run to produce a set of final output and converted from g/m^2 to Mg/ha for comparison with the biomass data from my field plots. These were then compared to field-measured biomass data. Final model outputs did not match up perfectly to the field aboveground biomass data. I extracted the modeled species biomass data for the first timestep (at year 0), from the raster cells that aligned with eight different locations where I had collected field biomass data and compared model and field total biomass data (Figure 3A). I also tried running the model on only those eight raster cells, but the results from that test were not very different from that of the full model of all of UMBS's area. I also calculated the mean total biomass for each ecoregion from the model output and compared that to the mean total biomass per landform of the field plots (Figure 3B).

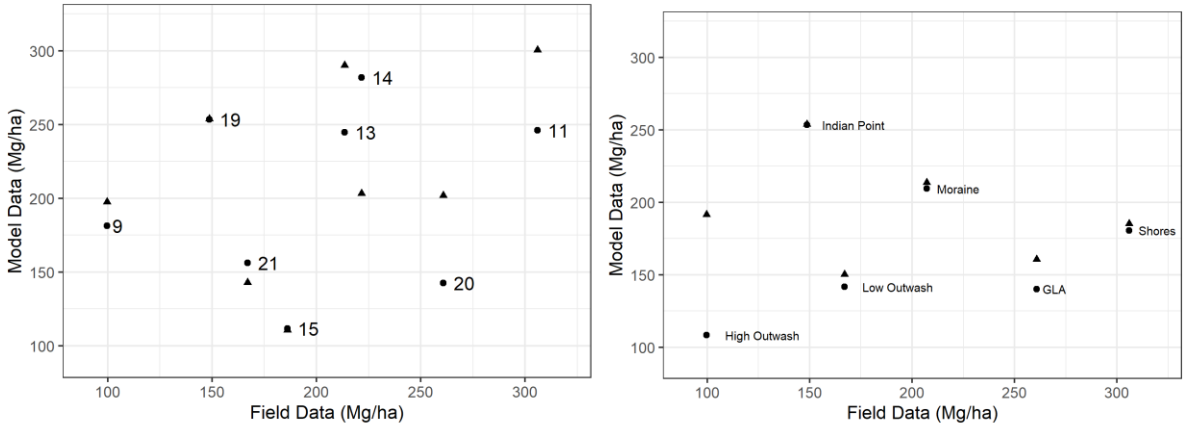


Figure 3. Figure 3A depicts the total biomass found at eight different field plots and the modeled results for the corresponding pixels, with stand number labeled. Figure 3b compares the mean total biomass found at each landform based on the field sites to the mean total biomass of each landform calculated from the model, with landform labeled. The circles represent model values generated from a lumped initial community map (see Figure 2a) and the triangles represent model values generated from a randomly generated community map (see Figure 2b).

The total biomass for all modeled sites were within the correct order of magnitude when compared to the field plots and the modeled high fertility ecoregions like the Moraine (excluding Indian Point) and the Shores/Ice Contact region did produce more biomass than low-fertility ecoregions like the High Outwash and Low Outwash. However, some field plots with low biomass overestimated biomass in the model, and some sites with high biomass were underestimated. This could be because most ecoregions were only represented by a single plot in the field data, potentially leading to bias if the sampled field plot is atypical in any way. For example, the model overestimated biomass at Indian Point Reserve, particularly oak biomass. The plot I sampled for species and age composition had a higher percentage of old-growth oak than the plot sampled for biomass. The way I generated the initial species communities for each raster cell is also not guaranteed to match up exactly to the species community present in the real-world location.

3.9 LANDIS-II Model Runs and Analysis

The LANDIS-II models were run using the PNet extension for the three climate scenarios on the four separate input maps for a total of twelve unique combinations. Each of those combinations was run with five times each for replicability. No other extensions were used. The four separate input maps were the uniform initial communities map, the random initial communities map, the uniform initial communities map with hickory added, and the random initial communities map with hickory added. Above ground biomass estimates were output for each raster cell (model 'site') as a result. The output was analyzed to see how species biomass changed over time and across climate and ecoregion using R. These four input maps—uniform, random, uniform-hickory, and random-hickory constituted the main divisions for analysis of the data. The output for different climate scenario runs were compared to the other climate scenario results run on the same input map. The five model replicates for each combination were averaged together to minimize the effect that random variance could have on the LANDIS-II output. The total mean aboveground biomass for all of UMBS was calculated. The means and standard deviations of species aboveground biomass were calculated for each ecoregion at each timestep, for each scenario/input map combination, so that I had the mean biomass for each species over time for every combination of model input. These means were compared to each other and plotted on a graph to visualize how each species changed over time under each climate scenario. Indian Point Reserve was separated from the rest of the Moraine ecoregion for the purposes of analysis due to its different land-use history and age structure.

4 RESULTS

4.1 Current Species-Age Cohorts at the UMBS

As of the 2019, the year of field data collection, the dominant overstory species in all ecoregions, except for the Low Outwash, was bigtooth aspen (Appendix Table J). Most individuals were between 80 and 100 years of age, which coincides with the last major fire in 1923 and the beginning of fire suppression at UMBS in 1935 (Barnes 1966, Barnes 2010, Gates 1930, Kilburn 1957). The size of these aspens was highly variable and depended greatly on the ecoregion. The aspens were at their largest in the more fertile Ice Contact and the Moraine ecoregion, with the largest individual measured at 77.1 cm dbh in the Ice Contact ecoregion (mean 40.39 cm dbh, mean age 88.44 years). In the poorer soil of the High Outwash, the mean dbh of bigtooth aspen, although similar in age at 87.78 years, was 25.78 cm dbh. Bigtooth aspens on the Glacial Lake Algonquin ecoregion were not as large as the Moraine and Ice Contact, but larger and more numerous than the High Outwash ecoregion.

The composition of the understory and of subdominant species also varied by ecoregion. The subdominant species in the Moraine and Ice Contact regions were broad-leaved trees. Both landforms contained beeches, northern red oak, red maples, and sugar maples that were a similar age to the bigtooth aspen at their oldest, but smaller in diameter. The mean dbh of red maple in the Moraine was 19.03 cm, sugar maple 13.30 cm, and beech 10.41 cm, while bigtooth aspen was 33.83 cm dbh. Aspen in the Moraine were, on average, 81.75 years old, red maple 77.56 years old, sugar maple 66.54 years old, and beech 82 years old. Although there are younger cohorts of these subdominant trees, particularly the sugar maple, the age structure of these trees was similar to bigtooth aspen, with then majority falling within the same age range (Figure 5). A similar pattern with regards to dbh and age occurred in the Ice Contact ecoregion, although there beech had the youngest average age. Beech and sugar maple were more abundant in the moraine. Mature red oak was present but sparse in both ecoregions and red maple was abundant in both ecoregions. The Ice Contact ecoregion also had rare basswood and adult ash trees.

The understory of the Moraine ecoregion continued to be dominated by deciduous species, but rarely by aspens. Seedlings, saplings, and young trees of red oak, sugar maple, red maple, and beech were common. The Ice Contact ecoregion, however, had few young oak trees or sugar maple past the seedling stage, while it also had several white pines growing in the understory. Beech saplings were very abundant on the Moraine ecoregion.

There was a wide age range of red oak present in the Moraine. The oldest red oak in the Moraine ecoregion outside of Indian Point Reserve was 91 years old, but there were many young trees in the 20–40-year age range as well. Indian Point Reserve, which was analyzed separately due to its separate land-use history, had the oldest trees of any plot sampled. The plot in Indian

Point was the only one where trees older than a century were common, with the oldest being a 176-year-old oak. It was dominated by old oak, beech, maple, and hemlock, and did not have much of a succeeding understory.

The subdominant species of the High Outwash and Glacial Lake Algonquin landforms, in contrast, included both broadleaved and coniferous species. The most common subdominant deciduous species were red oak and red maple, with few of the beech and sugar maple that were present in the Ice Contact and Moraine. The age of these trees was once again similar to that of the aspen, and the age of the last disturbance. There were even a few birch present, although birch was a rarer species at UMBS mostly observable in the form of fallen birch trunks.

The subdominant coniferous species of the High Outwash and Glacial Lake Algonquin ecoregions were white pine and red pine. The red pine was largely located on former plantations within the Glacial Lake Algonquin area. They tended to be between 50-70 years old and date back to when the UMBS property was used for forestry experiments (Barnes et al. 2010). White pine is present in both Glacial Lake Algonquin and the High Outwash, although it is more abundant in the Glacial Lake Algonquin ecoregion. The age cohort of white pine in both ecoregions was young, with few individuals over the age of 60. White pine was also very common in the understory. Although there were seedlings and saplings of red oak, red maple, and red pine present, white pine was the most abundant and many white pine trees had succeeded to the overstory.

Red pine, white pine, red oak, and bigtooth aspen were all more abundant in the Glacial Lake Algonquin ecoregion than in the High Outwash. Red maple was common in both. Although the mean diameter for bigtooth aspen was similar in both ecoregions (25.78 cm dbh in the High Outwash and 28.8 cm dbh in Glacial Lake Algonquin), Glacial Lake Algonquin had a larger range of sizes, from 13.1-45.3 cm dbh, whereas in the High Outwash bigtooth aspen sizes ranged from 17-36.9 cm dbh. There were also more overstory trees total in Glacial Lake Algonquin ecoregion. Mature red oak formed a significant component of the overstory and in some stands was the dominant species.

The Low Outwash landform was the only landform in which bigtooth aspen did not dominate the overstory. Here, both bigtooth aspen and trembling aspen were present, but neither formed the overstory. In addition, the aspen in the Low Outwash tended be younger than aspen elsewhere, with smaller diameters for their age, evenly spread between 40-80 years in age, with no age dominating. There were also 70-90 year old birches present.

The overstory of the Low Outwash, where it was present, was composed of old-growth pine. There were red pines and white pines that were over 100 years old, remnants that survived the logging era (Barnes 2010). The subdominant species consisted of a succeeding cohort of white pine, red pine, and red maple. The oldest white pine in this succeeding cohort was approximately 60 years old, but every age younger than that was represented. Red pine was somewhat less common, but still represented. The oldest red maple in the Low Outwash was approximately 80 years old, dating to the last disturbance (c. 1935), but many younger red maple were present as well. The youngest trees in the understory include balsam fir and white spruce, which are only found in our field samples on this landform as young trees, in addition to the pines and red maple.

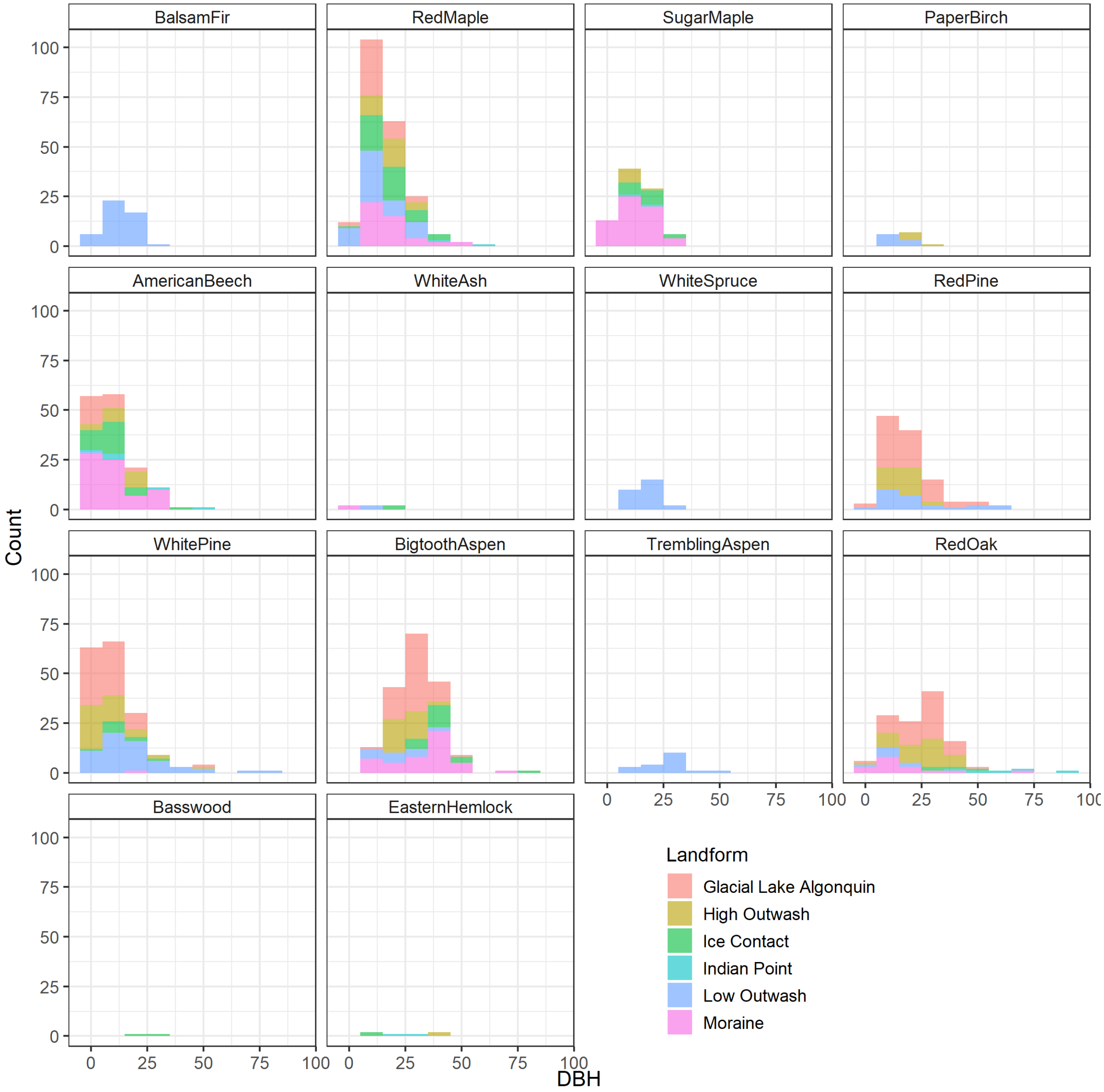


Figure 4: Shown is a histogram of overstory tree DBH at UMBS, separated by species and LANDIS-II ecoregion (based on Pearsall's (1995) landforms, with Indian Point Reserve separated due to land-use history. All measured trees from the field plots used in analysis are included.

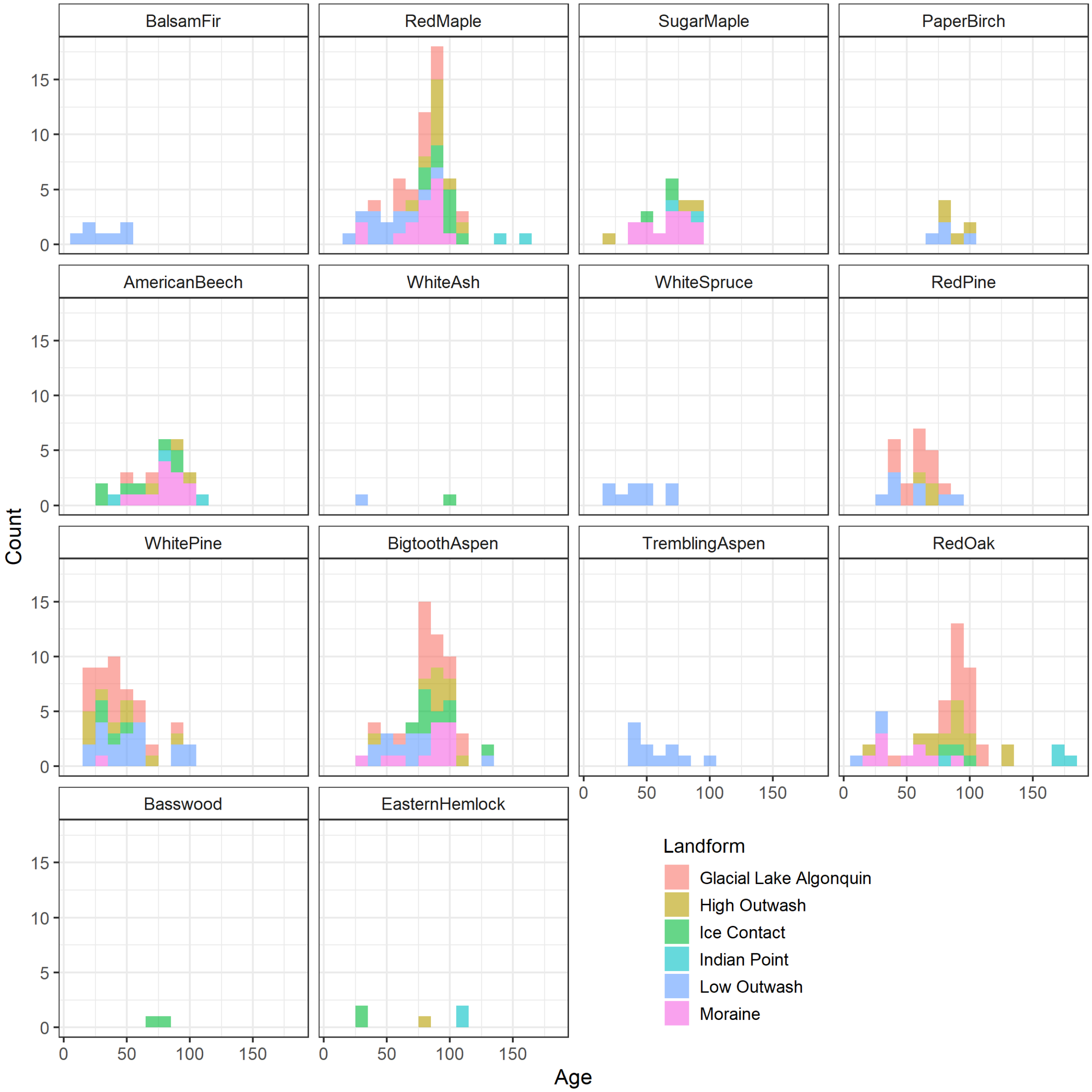


Figure 5. Shown is a histogram of tree age at UMBS, separated by species and LANDIS-II ecoregion (based on Pearsall's (1995) landforms, with Indian Point Reserve separated due to land-use history. Only the subset of trees measured for age and with readable cores are included.

4.2 Climate Predictions at UMBS

The annual mean maximum air temperature for January was -4.59 °C in the historical climatology, −3.05 °C in the current climatology, 0.13 °C in the RCP 4.5 scenario at the end of the 21st century, and 2.7 °C in the RCP 8.5 scenario at the end of the 21st century. The mean maximum air temperature for July was 25.69 °C in the historical climatology, 25.75 °C in the current climatology, 28.43°C in the RCP 4.5 scenario at the end of the 21st century, and 31.42 °C in the RCP 8.5 scenario at the end of the 21st century. The historical temperature climatology of a century ago and current climatology are very similar, although the current climatology is slightly warmer. The mean minimum air temperature follows the same trend. The RCP 8.5 and 4.5 climate scenarios have higher minimum and maximum temperatures than the current climate and historical climate. The RCP 8.5 climate scenario has higher temperatures than the RCP 4.5 climate scenario. Precipitation levels are far more variable, but in general they show an increase in precipitation during the winter, early spring, and fall, and a decrease in precipitation during the summer. This could be due to an increased amount of precipitation falling as rain.

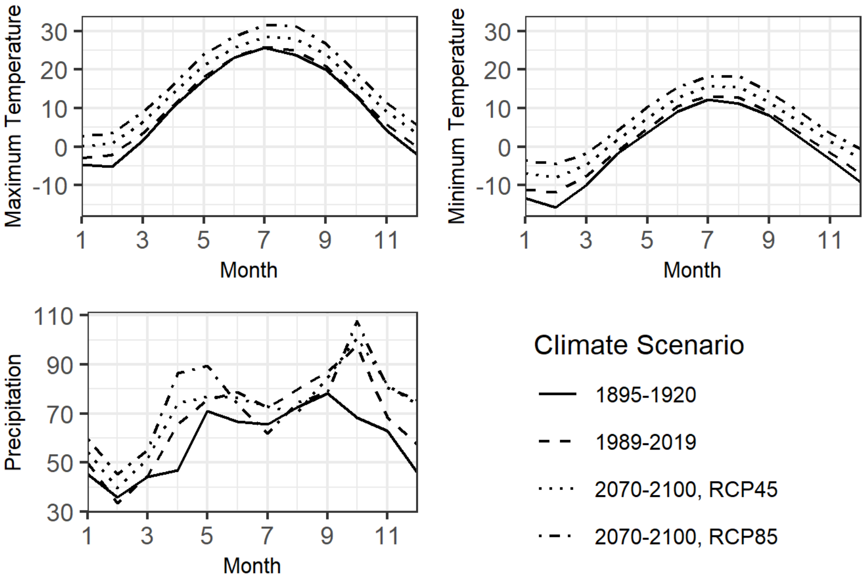


Figure 6. Mean maximum temperature (degrees C), minimum temperature (degrees C), and precipitation (mm) climatology for historical, contemporary, and two different modeled future time periods, RCP45 and RCP85.

4.3 Modeled Species and Biomass Change Under Different Climate Scenarios

At the beginning of all four model run versions run with the four separate input maps, aboveground biomass over the entire UMBS landscape was similar under all three climate scenarios. After an initial decrease, total biomass levels increased slightly under the base climate scenario and increased significantly under the RCP 8.5 climate change scenarios. At the end of all model runs, the scenario with the highest biomass increase was the high warming scenario, while the total biomass for the moderate warming scenario and the base climate scenario were similar, though the moderate warming scenario tended to be slightly higher (Figure 6). The total biomass for the model run versions that used a randomly distributed community map version was higher than the map with the evenly distributed community map version by about 500 Mg/m^2. Including hickory as an understory species did not lead to any significant changes in biomass. Aboveground biomass in Mg/ha was highest in Indian Point Reserve, which was analyzed separately from the rest of the Moraine, followed by the rest of the Moraine and Ice Contact ecoregion. The High Outwash ecoregion consistently had the lowest biomass, and the biomass of the Glacial Lake Algonquin ecoregion and Low Outwash ecoregion tended to be similar, although which one was higher depended on the model run.

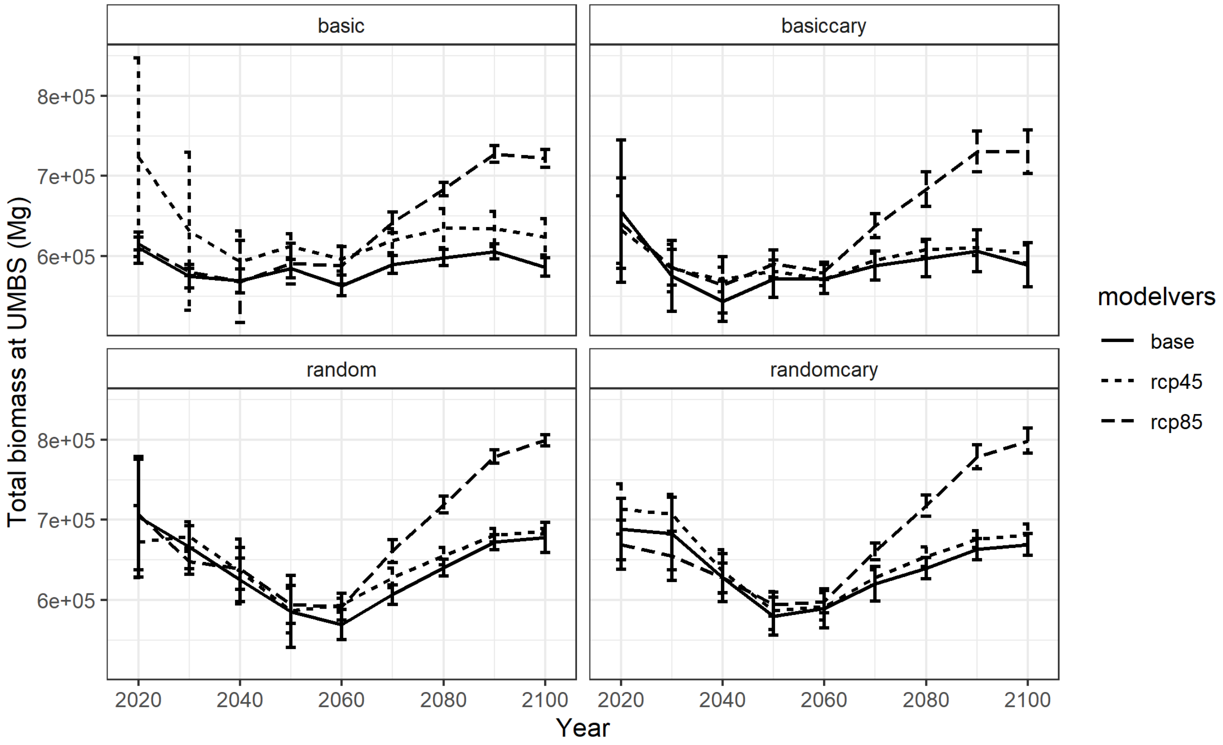


Figure 7: Total aboveground biomass (Mg) for the entire UMBS study landscape under three different climate scenarios. Figure A depicts biomass using uniformly distributed communities. B depicts biomass using randomly distributed communities. Figure C depicts biomass using uniform communities and a hickory understory in some community types at UMBS. D depicts biomass using a randomly distributed community and a hickory understory in some community types at UMBS. Hickory was included to test the range extensibility of a more southern species not currently present at UMBS.

Bigtooth aspen, trembling aspen, and paper birch decreased across all landforms between 2020 and 2100 under all climate scenarios and model runs. (Figure 8). These early successional species persisted longest in the Low Outwash area, and paper birch showed a slight increase between 2060 and 2080, although its biomass did not reach the same level as in 2020 (Appendix Figure G).

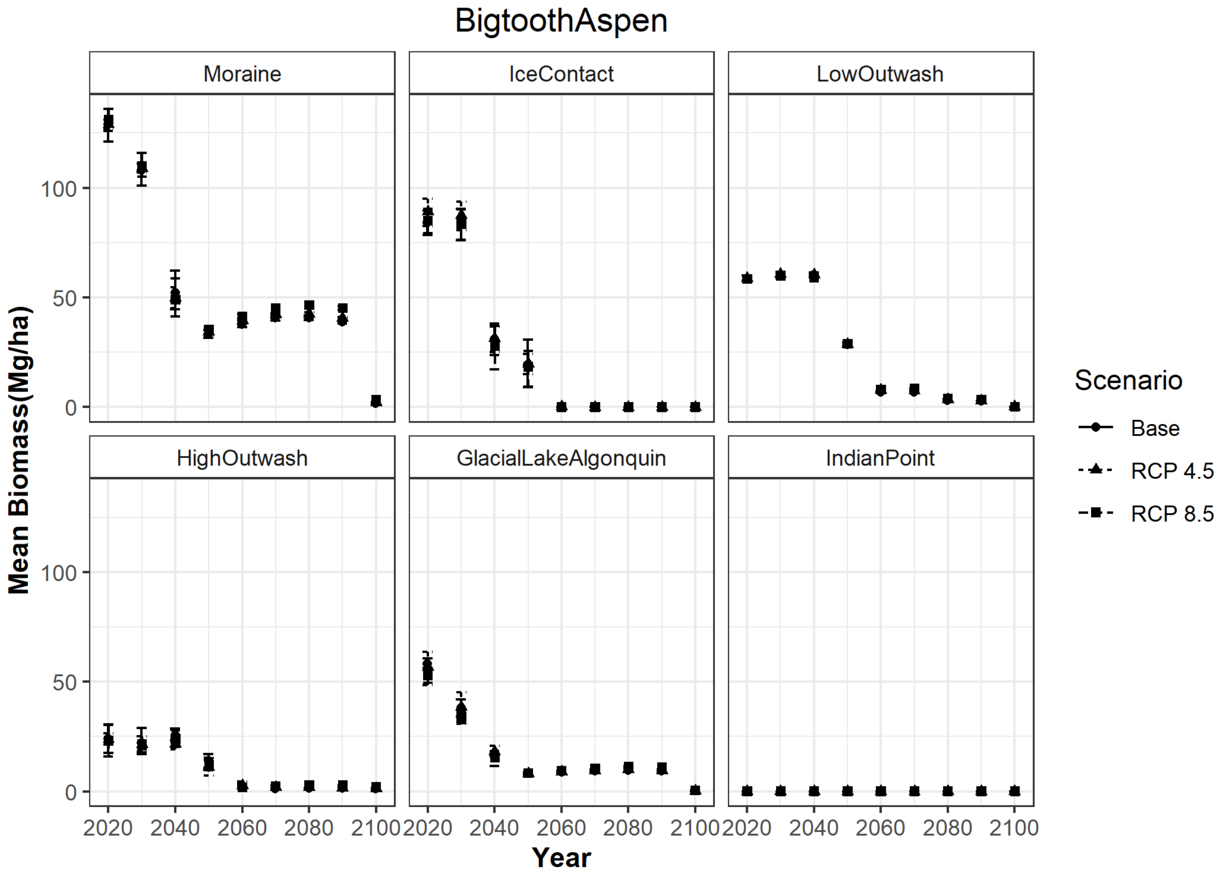


Figure 8: Bigtooth aspen biomass from 2020 to 2100 under three different climate scenarios, using the mean output of fifteen LANDIS-II model runs (five per scenario) with the randomly generated input map version. The climate scenarios include a low (base) climate change scenario, a medium climate change scenario (RCP4.5) and a high climate change scenario (RCP 8.5).

In general, the mid-successional and late-successional species increased in biomass where they were present (Appendix Figure G). Red maple was the only mid-successional species that clearly decreased by the end of all LANDIS-II model runs. Although it is present in all ecoregions, and currently forms a large part of the understory in the plots where it is present, during the course of the model it increases, peaks mid-century, and then gradually declines (Figure 9). Both the RCP 4.5 and RCP 8.5 climate scenarios led to increases in red maple's aboveground biomass in the model runs using both the randomly generated and the uniform input maps, particularly in the High Outwash and Moraine ecoregions (Appendix Figure G).

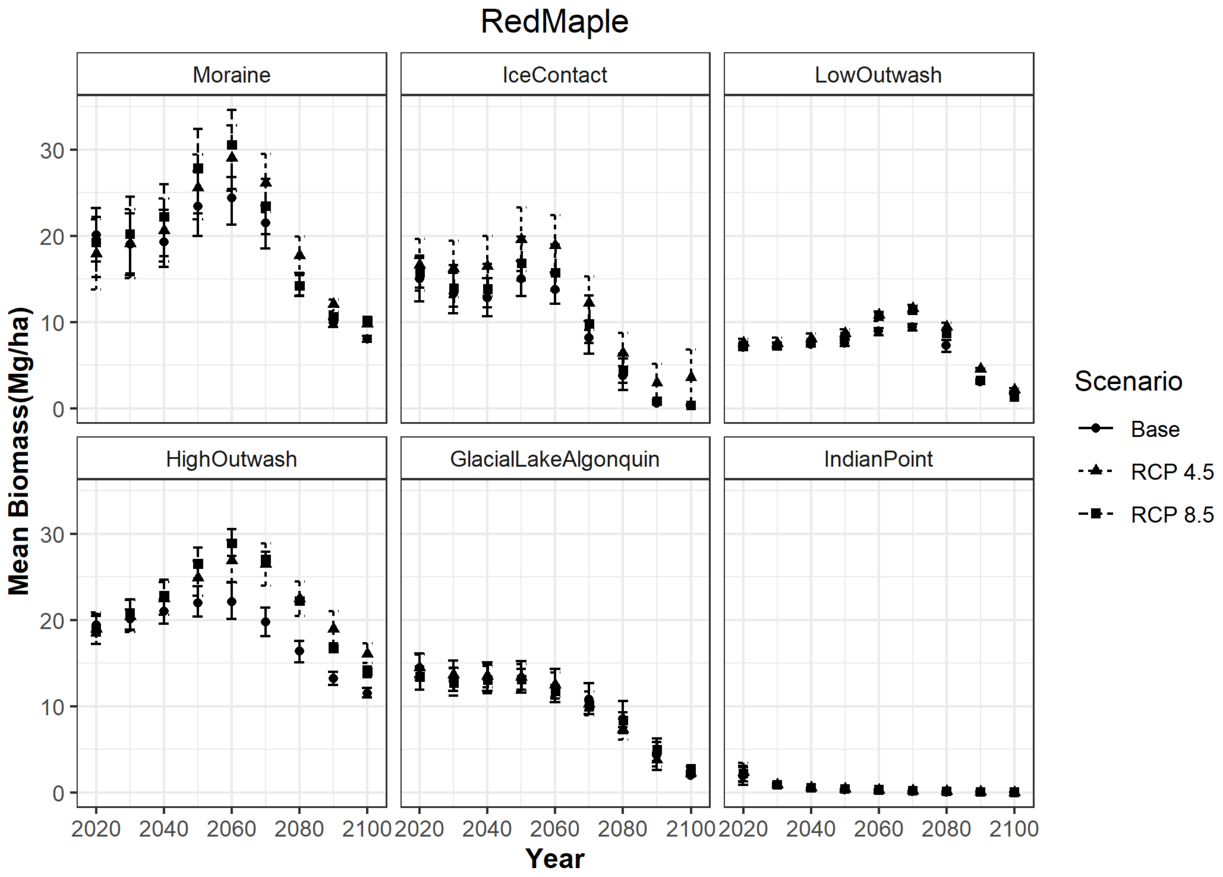


Figure 9: Red maple from 2020 to 2100 under three different climate scenarios, using the mean output of fifteen LANDIS-II model runs (five per scenario) with the randomly generated input map version. The climate scenarios include a low (base) climate change scenario, a medium climate change scenario (RCP4.5) and a high climate change scenario (RCP 8.5).

Sugar maple and beech are both late-successional species. Sugar maple is found mainly in the Ice Contact and Moraine ecoregions and beech is mainly found in the Moraine and High Outwash. Although beech saplings are widespread, they don’t survive to contribute significant biomass in other regions. Both of these species increase their biomass over the course of the LANDIS-II model runs with both the random and uniform input maps. Both species exhibit some increase in biomass under the RCP 4.5 and 8.5 climate change scenarios. Sugar maple biomass was significantly higher under the RCP 8.5 scenario compared to the base climate by the end of the model run and slightly higher under the RCP 4.5 scenario using both input maps. Beech significantly increased under both the RCP8.5 and RCP 4. 5 scenarios when compared to the base climate using the uniform input map and under RCP 8.5 in the random input map. This occurred around 2080 for both species. (Appendix Figure G).

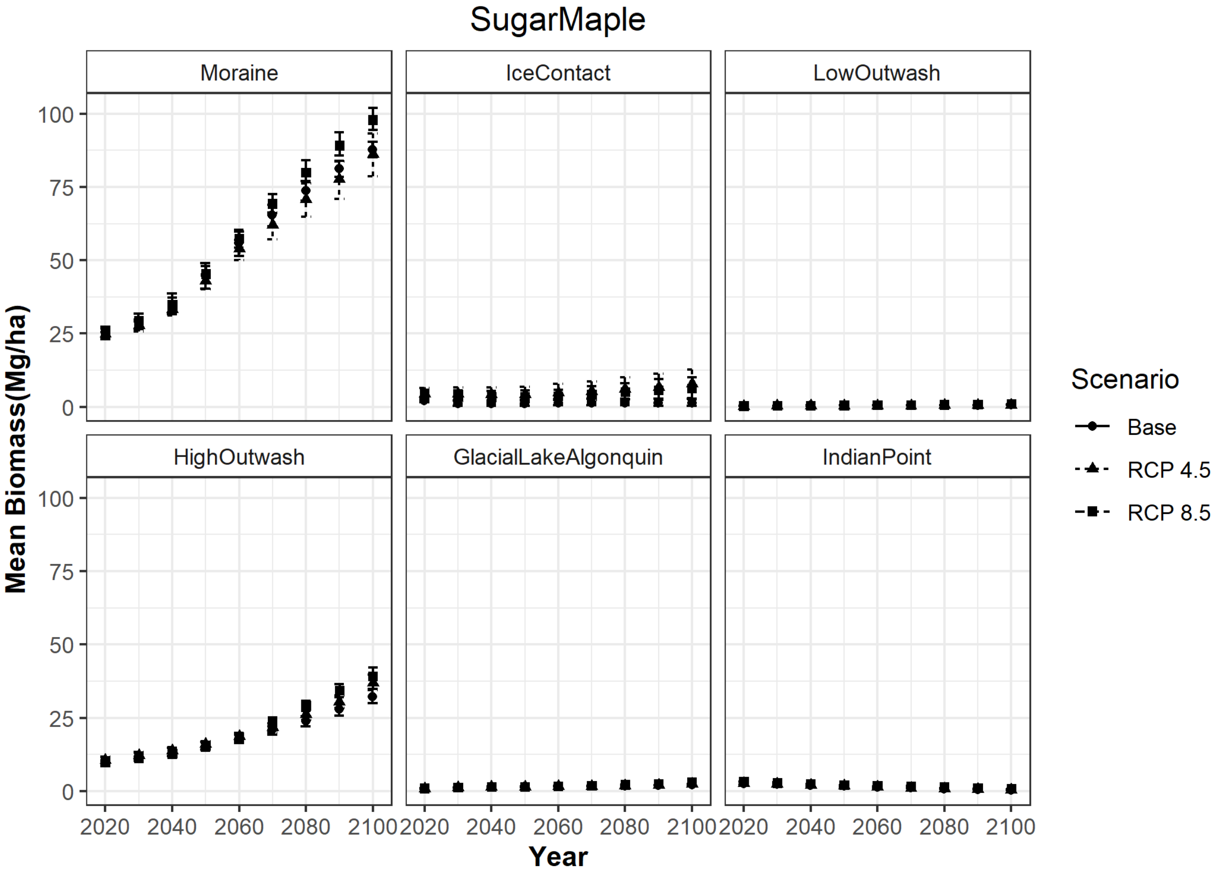


Figure 10: Sugar maple from 2020 to 2100 under three different climate scenarios, using the mean output of fifteen LANDIS-II model runs (five per scenario) with the randomly generated input map version. The climate scenarios include a low (base) climate change scenario, a medium climate change scenario (RCP4.5) and a high climate change scenario (RCP 8.5).

Currently, northern red oak is found on several UMBS ecoregions. It is a component of the richer Moraine and Ice Contact/Shoreline forests, and common in the drier High Outwash plain and Glacial Lake Algonquin. It is also present in Indian Point Reserve in the form of an old-growth stand due to Native American farming practices. During the model run, oak biomass increased at all locations except for Indian Point Reserve. In the High Outwash, oak increased significantly under the RCP 8.5 scenario, while at Indian Point Reserve, oak biomass decreased less under RCP 8.5 than in the other scenarios (Figure 11). This occurred in the model runs using the uniform input map and the random input map.

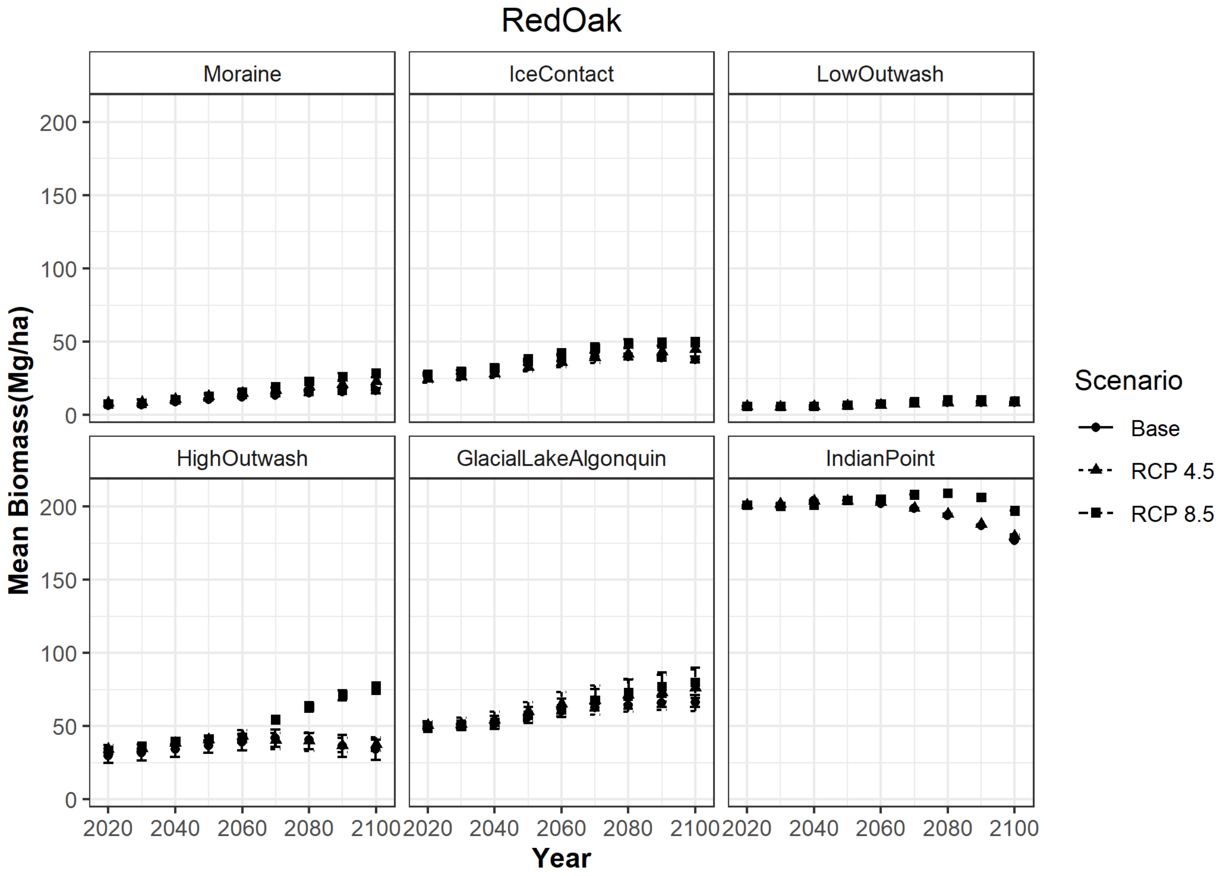


Figure 11. Red oak from 2020 to 2100 under three different climate scenarios, using the mean output of fifteen LANDIS-II model runs (five per scenario) with the randomly generated input map version. The climate scenarios include a low (base) climate change scenario, a medium climate change scenario (RCP4.5) and a high climate change scenario (RCP 8.5).

White pine is primarily found in the Low Outwash, High Outwash, and Glacial Lake Algonquin, with seedlings and young trees present in the Ice Contact region. Over the length of the LANDIS-II model runs with the random and uniform input maps, white pine increases in biomass in all ecoregions where it is present. The rate of increase is much smaller in the less-fertile High Outwash compared to the other landforms. The increase is also largest under RCP 8.5 than the other scenarios (Figure 12).

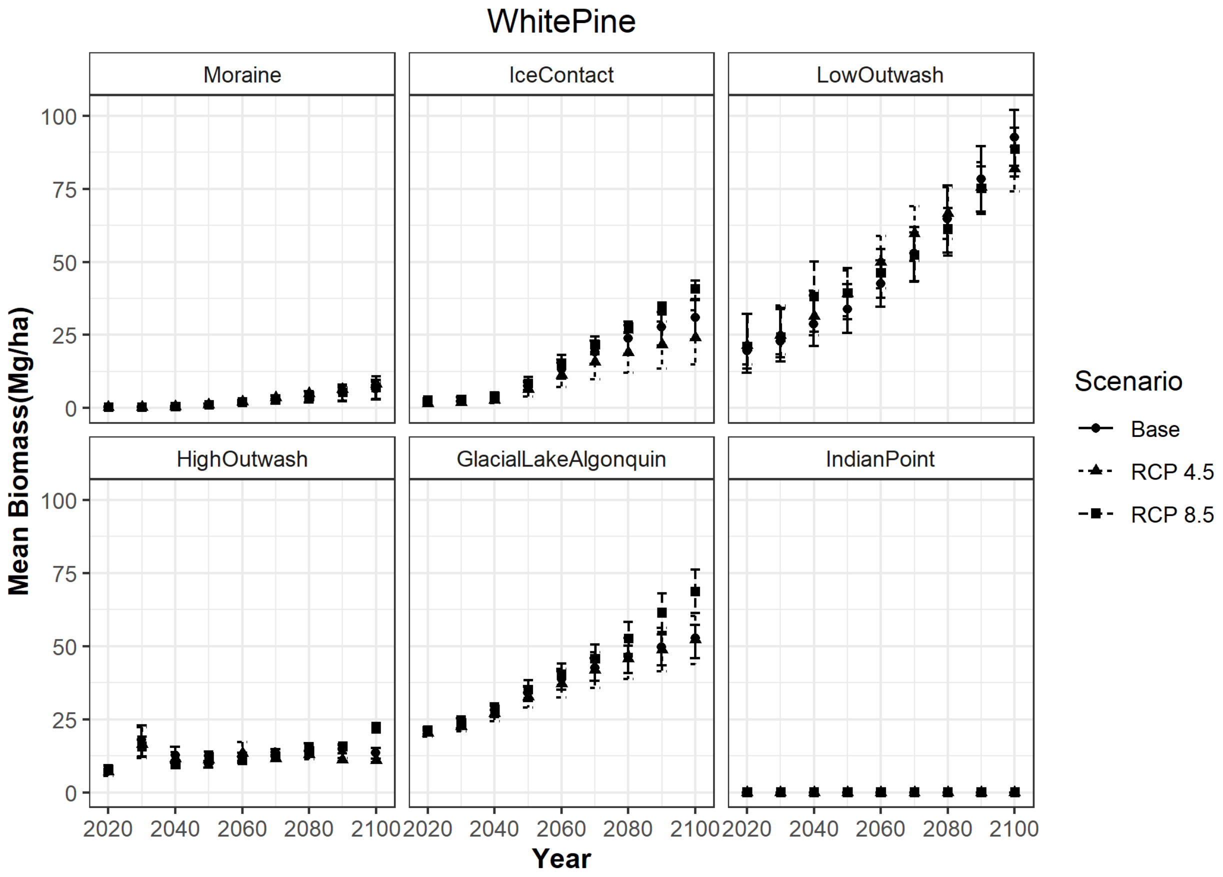


Figure 12. White pine from 2020 to 2100 under three different climate scenarios, using the mean output of fifteen LANDIS-II model runs (five per scenario) with the randomly generated input map version. The climate scenarios include a low (base) climate change scenario, a medium climate change scenario (RCP4.5) and a high climate change scenario (RCP 8.5).

Red pine shows extremely variable responses to climate (Appendix E). In the Low Outwash, biomass estimates did not increase much under any scenario in the model run using the random input map. However, when using the uniform input map, Low Outwash red pine biomass estimates are higher and biomass increased more over time, especially under RCP 8.5. In the High Outwash, it is difficult to tell whether or not biomass is increasing or decreasing, as the estimates are highly variable. In Glacial Lake Algonquin, the biomass increases over time in the model runs with both the uniform and random input maps. The increase is significant particularly under RCP 8.5 using the random input map.

White spruce and balsam fir are only found in the Low Outwash and the total biomass increases over time for both these species. Global warming led to increased growth and biomass for balsam fir, with the increase highest for RCP 8.5. This occurred in the model runs with the random and uniform input maps (Figure 13). Using the uniform input map, white spruce biomass increased the most under RCP 4.5, with RCP 8.5 having the lowest biomass. However, using the random input map, white spruce biomass only increased slightly under climate change, and there was not much difference between RCP 4.5 and RCP 8.5.

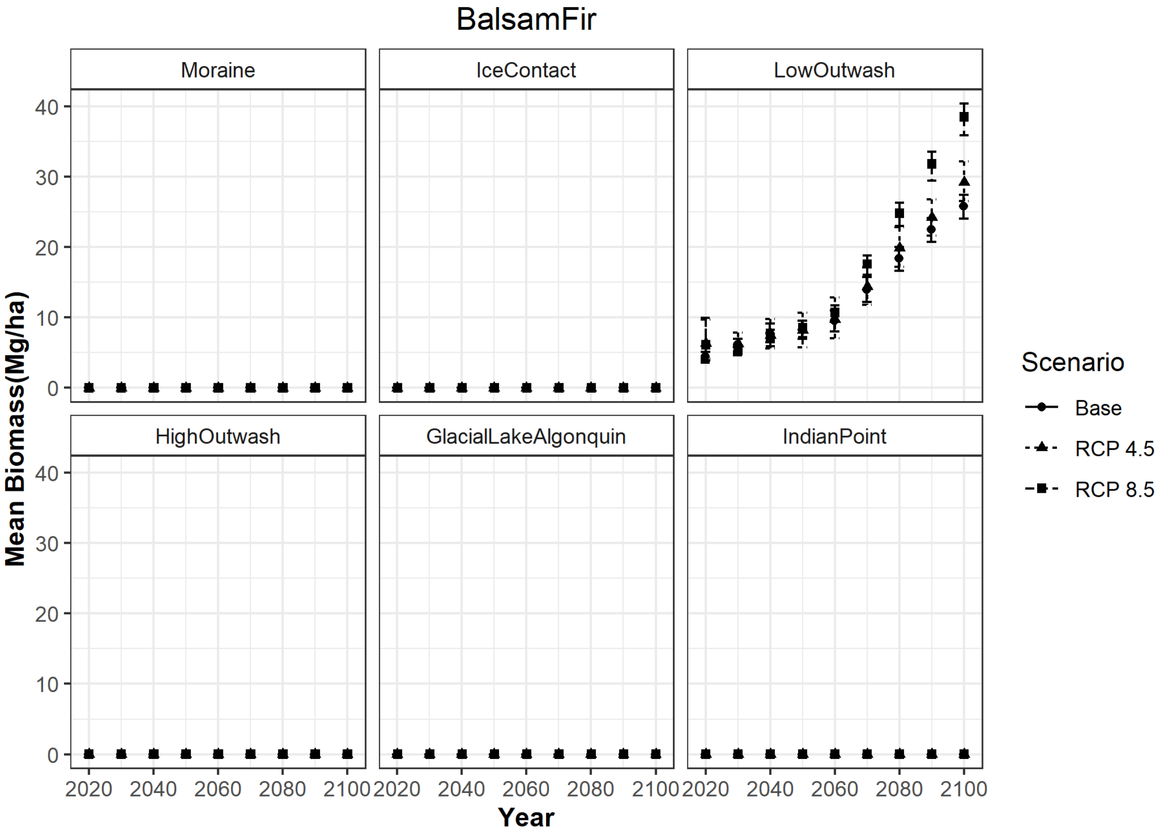


Figure 13. Balsam Fir from 2020 to 2100 under three different climate scenarios, using the mean output of fifteen LANDIS-II model runs (five per scenario) with the randomly generated input map version. The climate scenarios include a low (base) climate change scenario, a medium climate change scenario (RCP4.5) and a high climate change scenario (RCP 8.5).

There are very few old hemlock trees remaining except at Indian Point Reserve, although there are a few younger saplings along the shores of Douglas Lake. In the model, the hemlock trees in Indian Point Reserve increase in biomass, and do benefit from increased climate warming under RCP 8.5, though not RCP 4.5. The young hemlock trees in the Ice Contact region increase in biomass, and do significantly benefit from climate warming in the RCP 4.5 and RCP 8.5 scenarios.

American basswood is not a species present in great quantities in the landscape. There are a few adult trees in the Ice contact region and a few saplings in the moraine. Biomass increased in all model runs using both input maps and all climate scenarios, but the degree was highly variable due to its low presence on the landscape. There is no significant difference between the climate change scenarios, though biomass under the RCP 4.5 scenario was slightly higher than the base climate scenario and slightly lower than the base climate scenario under RCP 8.5.

Shagbark hickory showed a similar pattern. This species is not currently present on the UMBS landscape, but was added in in model simulations to see how a common more southern species would do if transplanted or through migration. It was added in as a seedling and left to grow. Like basswood, it did not become a major component of the landscape, but biomass increased more under the RCP 8.5 scenario's high warming, though not RCP 4.5's moderate warming.

Ash is another somewhat uncommon species on the UMBS uplands. While it was once prevalent, especially in more wetland areas, old growth ash is now only located in the ice contact area, with seedlings in the moraine and low outwash. Its biomass in the ice contact region is likely an overestimate. Nonetheless, biomass does increase more under RCP 8.5 when compared to the base and RCP 4.5 climate change scenarios.

5 DISCUSSION

5.1 The Effects of Climate Change at UMBS

Contrary to my hypothesis, modeling results showed that climate change did not lead to substantial shifts in study area forest community composition by the end of the 21st century. Succession was the primary driver of changes in biomass, however climate change did affect the magnitude of that change. The increase in biomass under high-warming scenarios is similar to that of other LANDIS-II models in the United States (Scheller and Mladenoff 2005, Wang et al. 2017) although Duveneck et al. (2014) found a decrease in biomass in Northern Michigan under high global warming due to the loss of boreal tree species. Succession, particularly aspen decline (Lucash et al. 2018), has also been found to play a more significant role than climate change in species composition (Wang et al. 2017). However, my model did not show a decline in boreal tree species that some other studies found (Duveneck et al. 2014, Lucash et al. 2018, Scheller and Mladenoff 2005, Wang et al. 2017). This could be because my model run only extended to 2100, whereas many of these other studies ran models for more than a century. Another possibility is that these boreal species like balsam fir and white spruce do not constitute enough of the upland UMBS landscape to significantly affect the results. Other researchers have found that Canadian forests may be more affected, as boreal tree species make up a larger proportion of the forest composition (Boulanger et al. 2017).

The largest effect of climate change at UMBS was the increase in biomass. The scenario with the highest emissions (RCP 8.5) consistently produced more biomass than the moderate warning and base climate scenarios. This effect was not due to one species benefiting from climate change, but rather a wide variety of species all exhibiting greater biomass accrual in that scenario. White pine, red maple, sugar maple, and northern red oak all increased more under climate change, as well as lesser components of the landscape like hemlock and balsam fir. Other models have shown that as long as climate change does not lead to water stress, productivity in northern forests will increase (Motew and Kucharik 2013, Ollinger et al. 2008, Pastor and Post 1988, Peters et al. 2013). One of the few species to show less biomass under the high warming scenario compared to the base climate was red pine in the high outwash, the driest landform at UMBS. Many of these pines are also the result of experimental plantations at UMBS, and not natural growth.

5.2 Effects of Landform on LANDIS-II Biomass Estimates

A geological landform is a discrete area with similar parent material and topography. These underlying physical characteristics affect the soil and water and nutrient availability, which, in turn, greatly affect the species growing on that landform (Pearsall 1995). In the Upper Great Lakes, most landforms are the results of glacial process on the landscape. Therefore, landforms are ecologically significant units of analysis. It affects species composition, species richness, seedling recruitment and succession (Bergen and Dronova 2007, Host et al. 1987, Ricart et al. 2020, Schreeg et al. 2005) and net primary productivity and biomass accumulation (Dronova et al. 2011, Host et al. 1988, Nave et al. 2017, Zak et al. 1989). When parameterizing the LANDIS-II model, I used the glacial landforms from Pearsall (1995) as ecoregions with different physical soil parameters. The collection of field data was stratified between ecoregions, and ecoregion determined the initial community composition. Given that ecoregion, and therefore landform, played a large role in initializing and parameterizing the model, it is not surprising that landform also affects the results. My initial biomass estimates across all model runs for the Moraine ecoregion are similar to the results of other studies using field data from moraine landforms at UMBS and other sites across the Upper Great Lakes region. Moraine aboveground biomass estimates from LANDIS-II varied slightly between model runs, but the mean aboveground biomass was 212.28 Mg/ha, comparable to estimates from Host et al (1988), Zak et al. (1989), and Dronova et al. (2011). Aboveground biomass estimates for Ice Contact also fell within the range of variation of published values. However, High Outwash aboveground biomass estimates were consistently higher than my own field data as well as published figures for aboveground biomass in outwash landforms. There was also a high degree of variability between model runs, with sharp differences between my basic and random model runs (Figure 3). The biomass estimates for the Glacial Lake Algonquin and Low Outwash ecoregions were also higher than the published figures for outwash landforms, however, my field data also showed higher biomass in those ecoregions. Indian Point Reserve had the highest LANDIS-II aboveground biomass estimates, higher than the field data I collected, around 250 Mg/ha. Zak et al. (1989) found similar biomass in a mature northern hardwood forest located on a moraine, which is the same community type and landform as Indian Point Reserve. Mature forests on mesic sites could even accumulate biomass up to 300-400 Mg/ha (Nave et al. 2017).

5.3 Successional Changes at UMBS

The largest observable change from the initial conditions of the model run, which occurred in all ecoregions under all climate scenarios, was the conversion of forest from one dominated by early-successional aspen and birch to one dominated by a variety of mid- to late-successional species that are currently in the subdominant overstory and understory. The decrease in biomass mid-century in model output is due to high mortality among remaining over-mature aspen. This trend has also been observed in other LANDIS-II model runs in northern Michigan and the Upper Midwest (Duveneck and Scheller 2016, Lucash et al. 2018, Xu et al. 2012). The decline of aspen and replacement with mid- and late-successional species has also been observed experimentally at UMBS and elsewhere in the region (Bergen and Dronova 2007, Fahey 2014, Gough et al. 2010). Climate envelope models have predicted major losses in the available habitat for aspen-birch forests in the upper Great Lakes due to climate change (Iverson et al. 2008), but these forests may also be disappearing due to successional processes and lack of widespread fire disturbance. In fact, it is likely that they will disappear even faster than expected by the model, as bigtooth aspen died in most ecoregions at UMBS before 2040, due to the advanced age of the starting cohorts. None of the LANDIS-II disturbance extension were used, so the biomass of these early-successional aspen-birch species remained low throughout the course of the model run.

However, aspen persisted in the Low Outwash ecoregion longer. Bigtooth aspen in the Low Outwash are decades younger than in other ecoregions, and trembling aspen was not found in any study plots outside of the Low Outwash, where a large age range was found. The presence of young early successional aspen and still-living paper birch when most of them have already died out in the rest of UMBS suggests that the Low Outwash landform may be in an earlier successional state compared to the rest of UMBS. A study of trembling aspen clones at UMBS found that in 1981, trembling aspen ramets in the Moraine were older than trembling aspen ramets in the Low Outwash (Sakai and Burris 1985). The Low Outwash is also a climactically extreme environment that benefits trembling aspen over bigtooth aspen. Trembling aspen are more suited for cooler climate and poorly drained soils, physical conditions found in the Low Outwash (Barnes and Pregitzer 1984). The Low Outwash is less optimal habitat for bigtooth aspen, and no old bigtooth aspen were found in this ecoregion. It is possible that the bigtooth aspen in the Low Outwash may have a shorter lifespan due to the extreme conditions of the landform, as poor habitat can decrease aspen lifespan (Burns and Honkala 1990). If this is the case, then the bigtooth aspen in this ecoregion may die considerably earlier than the LANDIS-II results show. However, by mid-century, the LANDIS-II model showed a decrease in all aspen biomass in the Low Outwash, including trembling aspen.

Throughout the upper Great Lakes region, the mid- and late-successional species that will dominate its northern forests are not the same as pre-European settlement species. While many of the succeeding species dominated the forest prior to European settlement, some tree species and communities are failing to regenerate due to fire exclusion. (Fahey 2014, Friedman and Reich 2005, Hartman et al. 2005, Palik and Pregitzer 1992). Some species, including hemlock, are not regenerating, and others, in particular red maple (*Acer rubrum*) have expanded their range, so that forests of the future are unlikely to resemble forests of the past (Barnes 2010). The relative dominance of later successional species has also shifted compared to pre-European settlement vegetation. Species like red maple, sugar maple, and red oak currently make up a larger part of the forest ecosystem in the Upper Great Lakes than they did previously, particularly in the case of red maple (Barnes 2010, Fahey 2014, Whitney 1987, Palik and Pregitzer 1992). There are multiple factors that led to these changes. The repeated fires at the end of the logging era that led to the dominance of aspen-birch forests also allowed species like northern red oak and red maple to establish themselves from sprouts (Palik and Pregitzer 1992). The subsequent era of fire exclusion led to further changes as fire-adapted species like northern red oak failed to regenerate (Barnes 2010, Hartman et al. 2005, Nowacki and Abrams 2008). The removal of overstory species also changed seed rain distribution and changed the microclimate at the forest floor to a drier, more open environment (Palik and Pregitzer 1992). More recently, increased browse pressure from white-tailed deer prevents the regeneration of species like hemlock and oak (Alverson et al. 1988, Fisichelli et al. 2012, Granger et al. 2018).

My model results showed an increase in the amount of sugar maple and beech in the landforms where they were a significant part of the understory under all climate scenarios. The long time it takes for the effects of climate change to show with regard to these species is likely because both species are slow-growing and shade-loving (Burns and Honkala 1990). Field and other data have confirmed that the proportion of sugar maple has increased to date compared to the composition of pre- European settlement Michigan forests, in part due to its greater dispersal ability (Palik and Pregitzer 1992, Whitney 1987). While some models have predicted the loss of sugar maple in the United States (Iverson et al. 2008), experimental studies in Canada have shown increases in growth under warmer temperatures and increased colonization into boreal forests (Boulanger et al. 2017, Goldblum and Riggs 2002, Fisichelli et al. 2014). My results show that Northern Michigan will still be capable of supporting sugar maple through the end of the 21st century, however Duveneck and Scheller (2017) showed a decrease in sugar maple biomass under the high emissions run and increase under low emissions.

Like sugar maple, red maple seedlings have been colonizing boreal forests, and warmer temperatures tend to increase red maple growth rates. However, red maple is less shade-tolerant and shorter-lived than sugar maple (Burns and Honkala 1990), so over the course of the model run, it was outcompeted, with the highest red maple biomass occurring mid-century. Field and other studies have shown that in fact red maple has significantly expanded its range due to a unique combination of historical factors. For example, red maple was limited to swampy lowland areas in pre-logging forests, but has since expanded to become one of the most common species in eastern forests (Abrams 1998, Nowacki and Abrams 2008). This was caused by a combination of factors—the fires that swept the region after logging created a niche for red maple root sprouts to expand, and continued fire suppression led to those trees maturing (Palik and Pregitzer 1992, Abrams 1998, Nowacki and Abrams 2008). This dominance may not continue. The LANDIS-II results show a decrease in red maple biomass associated with age-related mortality.

Although total oak biomass decreased over the course of the LANDIS-II model, this was primarily due to mortality in the old-growth oak stands at Indian Point Reserve. Oak formed a large part of the community there due to Native American farming practices (Albert and Minc 1987). Northern red oak, and oaks in general, are expected to benefit greatly from climate change, and in particular a hotter, drier climate, as oak is more drought-tolerant than other hardwoods (Clark et al. 2016, Overpeck et al. 1991). My study found the amount of oak biomass outside of Indian Point Reserve increased slightly over time. The increase in biomass was particularly large in the High Outwash under the high climate change scenario. However, in the other regions, the rate of increase was much smaller. The High Outwash is the driest landform at UMBS, and water stress may give a competitive advantage to red oak that is not present in the other landforms.

Across the eastern United States, however, oaks are failing to regenerate, despite model predictions. The process of mesophication and fire exclusion has been implicated as a major reason why oaks are failing to regenerate throughout the eastern United States (Abrams 1998, Nowacki and Abrams 2008, Hanberry et al 2012.). In addition to species competition, deer browsing and frost are also significant barriers to oak regeneration (Buckley et al. 1998, Granger et al. 2018, Hartman et al. 2005). In Northern Michigan in general, northern red oak was not a major component of the overstory historically and it increased due to the large fires that occurred at the end of the logging era in the early 20th century (Barnes et al. 2010, Whitney 1987). At UMBS, oak was among the oldest trees to have established or survived the fires. Many of the oaks in the high outwash predated the last fire in 1923 (Gates 1930, Kilburn 1957) and survived it, with some tree cores showing fire scars. Red maple, which has been implicated as the primary competitor to red oak (Abrams 1998, Nowacki and Abrams 2008), is present in the same ecoregions as oak at UMBS. However, even after red maple decreases towards the end the model run, oak recruitment outside of the high outwash does not pick up in response. Red maple leaf litter can change the soil composition to favor its own recruitment, creating a positive feedback loop (Alexander and Arthur 2010). Oak seedlings may only benefit from increased temperature in high-light environments, compared to more shade tolerant maples (Fisichelli et al. 2012), so being shaded out could cancel the beneficial effect of warmer temperatures on growth. Another hypothesis is that it is being shaded out by white pine, which is found in the High Outwash and Glacial Lake Algonquin ecoregions in large numbers. These white pine trees are currently in the understory, but could overtop any oak saplings, being a faster growing species (Burns and Honkala 1990). Many studies have observed oak seedlings regenerating under pine stands, and pine seedlings regenerating under oak stands, leading to the hypothesis that these species cyclically replace each other (Crow 1988, Johnson 1992). Experimental planting of northern red oak seedlings shows the highest success under pine plantations, but only when protected from deer browsing (Buckley et al. 1998, Granger et al. 2018, Hartman et al. 2005). Supporting the idea that these two species are in competition with each other, in the model runs white pine does not increase as greatly in the High Outwash, whereas oak did increase. Despite the fears about the lack of oak recruitment, the field sampling for this project showed a number of 30–40-year-old oaks, and numerous saplings. Low shade tolerance could also explain why red pine does not do well in the model, despite being a major component of the forest during pre-European settlement times. Red pine is less shade tolerant than white pine (Burns and Honkala 1990).

White pine benefits from ongoing succession by increasing in biomass over the course of all LANDIS-II model runs. Much of the forest was dominated by white pine prior to logging in the 19th and early 20th centuries (Barnes 2010, Whitney 1987), and there are still a few remnant trees that are older than a century. Pine saplings and seedlings have been observed in the understory of aspen-dominated forests for years (Host et al. 1987, Peterson and Squiers 1995, Roberts and Richardson 1985). Similarly, most pine at UMBS are young and in the understory or sub-dominant canopy of the now over-mature aspen. White pine in these situations is poised for competitive release as the over-mature aspen die off and that is exactly what the increase in biomass in the model shows, particularly in Glacial Lake Algonquin and the Low Outwash. The lesser increase of white pine in the high outwash is likely because there is very poor soil overall, in addition to competition from oaks.

Balsam fir and spruce are boreal species and they are expected to decrease in the upper Great Lakes region as their range is expected to move north (Iverson et al. 2008, Swanston et al. 2018, Overpeck et al. 1991). In my model, however, biomass increased, and balsam fir biomass increased the most under the high climate change scenario. While balsam fir recruitment decreases in response to warmer temperature (Duveneck and Scheller 2016), the balsam fir in my model is already present in the landscape. Because the established species cohorts are very young, they accumulated biomass as they matured. Browse pressure from white-tailed deer on temperate competitors such as sugar maple, red maple, and red oak by deer could offset decreased growth under warmer temperatures in seedlings of these species (Fisichelli et al. 2012). The problem with boreal species is not that they can't survive in warmer climates, but that they don't grow fast enough. The northern limit of most temperate trees is located along the -40 C isotherm (Goldblum and Rigg 2010). Winter temperatures below this point, and freeze-thaw cycles in the early spring, lead to cold damage in species like sugar maple (Arris and Eagleson 1989, Brandt 2009). The southern limit for most boreal species, however, is not directly related to temperature (Bonan and Sirois 1992). Balsam fir can grow in warmer temperatures. Instead, this limit is where boreal species will be outcompeted by deciduous trees (Arris and Eagleson 1994, Goldblum and Rigg 2010). For example, the growth rate of sugar maple increases with warmer temperatures, while the growth rate of balsam fir decreases (Goldblum and Rigg 2005, Fisichelli et al. 2014). As a result, sugar maple is expected to thrive more under climate change in boreal regions. White spruce did show decreases in biomass under RCP 8.5, the highest climate warming scenario compared to RCP 4.5 in the LANDIS-II model run with a uniform input map, so there may be a limit to how much boreal species can benefit from climate change.

5.4 Potential Migration

Climate change may lead to the range expansion of species currently located further south of the Upper Great Lakes. In addition to the stability of boreal species, more southerly tree species like hickory increased, but remained a minor component of the forest. Both these species are expected to move north under climate change (Iverson et al. 2008). However, competition with established trees make it difficult for new seedlings to be established. Tree saplings migrate northward by establishing within gaps in response to changes in temperature (Fisichelli et al 2014, Kellman 2004, Leithead et al. 2010). However, microsite climatic factors and competition may limit northward establishment (Barras and Kellman 2002, Fisichelli et al. 2013, Fisichelli et al. 2014, Goldblum and Rigg 2005, Ibáñez et al. 2009). Although both potential migrants and local species benefit from growing in gaps (Ibáñez et al. 2009), southern migrants in Canada have been found to only establish in gaps, while local species establish in both the understory and in gaps equally (Leithead et al. 2010), which may suggest that migrants are not yet competitive. In one study, deer browsing eliminated the growth advantage temperate species had over boreal species (Fisichelli et al. 2012). Slow dieback of established northern tree species in forests can slow the advancement of southern species (Loehle 2000). Although hickory biomass increased in response to climate change in the LANDIS-II results, it does not become a major species.

5.5 Other Factors

The results of this study demonstrate the need to take into account land history and physical factors like landforms when accounting for the effects of climate change on northern forests. In general, none of the species colonized new areas or established in landforms where they had not previously been present. Local factors such as competition for light and soils resources also play important roles in preventing shifts in species composition that would otherwise be predicted by climate envelopes models (Clark et al. 2011, Ibáñez et al. 2006, Pederson et al. 2015).

Land-use history can cause important differences in the landscape, from shifts in species composition due to changes in fire regimes, (Hanberry et al. 2012, Nowacki and Abrams 2015). The effects of land-use history can overpower the effects of climate change that might otherwise show up on the landscape (Nowacki and Abrams 2015, Ollinger et al. 2002). In this study area, the Indian Point Reserve species composition and age structure remains unique throughout all LANDIS-II model runs when compared to other areas within the same landform due to its land-use history.

Disease is another important non-climate factor that can affect species distribution, and be affected by climate change, yet my model did not account for it. As a result, biomass estimates for beech (currently affected by beech bark disease) and ash (affected by emerald ash borer) are likely too high. Other models have found disease to be among the most important factors (Shifley and Moser 2016) when attempting to predict a locally-realistic future landscape, rather than predicting overall effects of climate warming irrespective of unique land-use history and disease.

6 CONCLUSION

This study modeled and investigated the multi-decade effects of three different climate scenarios on upland forests community composition and biomass at the University of Michigan Biological Station (UMBS). Study and modeling methods accounted for known underlying geology-soils factors (landform type) and known past land-use histories that are also widespread in other upper Great Lakes landscapes. This study did not include factors of present or future more stochastic disturbances such as those from insects, browsing, or fire.

Forest composition and biomass were modeled over an 80-year time period (2020 – 2100). In the models that I ran, few species showed decreases in biomass even under the highest climate warming scenario, RCP 8.5. The largest changes in species composition at UMBS were due to natural successional processes as old over-mature aspen die off and understory species succeed them. Climate change did increase the growth of several species, including maple, beech, oak, and pine. White pine benefited the most from both climate change and its position as a fast-growing species in the understory. The boreal species of balsam fir and white spruce also increased in biomass, contrary to my hypothesis. This is likely because at UMBS these trees have already established and are relatively young. Oak biomass increased slightly under climate change outside of Indian Point Reserve, although field studies show limited regeneration of oak in what may be part of a larger trend of mesophication. Southern species like hickory significantly increased under climate change, but did not become a major species in terms of biomass over the course of the model run. These results show the importance of factors outside of climate change, such as competition with already established species in the case of the boreal species and the hickory, land-use history and changed fire regimes in the case of the oak, and successional processes in the case of the aspen. At UMBS, in particular, disease is another important factor that should be included in further research in order to understand its future landscape composition above that due to climate change in absence of disturbances.

APPENDICES – TABLES

APPENDIX TABLE A

Landform	Covertype	Count	Plots	Final Covertype	Final value	Initial Value
Moraine	Aspen to N. Hardwoods	320	5, 23, 6, 22, 11	Moraine Aspen to N. Hardwoods	1	23
Moraine	Upland Conifer	8		Moraine Aspen to N. Hardwoods	1	28
Moraine	aspen to northern red oak-upland conifer	1		Moraine Aspen to N. Hardwoods	1	49
Moraine	aspen to northern red oak-red maple	2		Moraine Aspen to N. Hardwoods	1	50
Moraine	Aspen to N. Hardwoods/Upland Conifer	1		Moraine Aspen to N. Hardwoods	1	51
Moraine	Aspen to Upland Conifer	7		Moraine Aspen to N. Hardwoods	1	52
Moraine	N. Hardwoods	162	4, 41	Moraine N. Hardwoods	2	14
Moraine	Oak	3		Moraine N. Hardwoods	2	48
Shores&IceContact	N. Hardwoods	63	27	Ice Contact N. Hardwoods	3	8
Shores&IceContact	Oak	5		Ice Contact N. Hardwoods	3	30
Shores&IceContact	Aspen to N. Hardwoods/Upland Conifer	4		Ice Contact Aspen to N. Hardwoods	4	6
Shores&IceContact	Aspen to N. Hardwoods	105	30,31, 29	Ice Contact Aspen to N. Hardwoods	4	9
Shores&IceContact	aspen to northern red oak-red maple	8		Ice Contact Aspen to N. Hardwoods	4	11
Shores&IceContact	aspen to northern red oak-upland conifer	4		Ice Contact Aspen to N. Hardwoods	4	12
Shores&IceContact	Aspen to Upland Conifer	40	26	Ice Contact Aspen to Upland Conifer	5	5
Shores&IceContact	Upland Conifer	21		Ice Contact Aspen to Upland Conifer	5	7
Low Outwash	Upland Conifer	237	25,28	Low Outwash Upland Conifer	6	4
Low Outwash	Aspen to Upland Conifer	226	24, 40	Low Outwash Aspen to Upland Conifer	7	2
Low Outwash	Aspen to N. Hardwoods	215	12,33	Low Outwash Aspen to N. Hardwoods	8	1
Low Outwash	N. Hardwoods	30		Low Outwash Aspen to N. Hardwoods	8	3

Low Outwash	aspen to northern red oak-upland conifer	11		Low Outwash Aspen to N. Hardwoods	8	21
Low Outwash	aspen to northern red oak-red maple	5		Low Outwash Aspen to N. Hardwoods	8	22
Low Outwash	Aspen to N. Hardwoods/Upland Conifer	18		Low Outwash Aspen to N. Hardwoods	8	26
Low Outwash	Oak	6		Low Outwash Aspen to N. Hardwoods	8	32
High Outwash	N. Hardwoods	96	16	High Outwash Northern Hardwoods	9	29
High Outwash	Aspen to N. Hardwoods	264	1,2	High Outwash Aspen to N. Hardwoods	10	31
High Outwash	Aspen to N. Hardwoods/Upland Conifer	20		High Outwash Aspen to N. Hardwoods	10	38
High Outwash	Aspen to Upland Conifer	48	36, 38	High Outwash Aspen to Upland Conifer	11	37
High Outwash	Upland Conifer	13		High Outwash Aspen to Upland Conifer	11	40
High Outwash	aspen to northern red oak-red maple	26	3	High Outwash Aspen to Oak	12	34
High Outwash	Oak	30		High Outwash Aspen to Oak	12	35
High Outwash	aspen to northern red oak-upland conifer	25		High Outwash Aspen to Oak	12	36
Glacial Lake Algonquin	Aspen to N. Hardwoods	85	13,14	Glacial Lake Algonquin Aspen to N. Hardwoods	13	43
Glacial Lake Algonquin	N. Hardwoods	17	32	Glacial Lake Algonquin Aspen to N. Hardwoods	13	44
Glacial Lake Algonquin	Aspen to N. Hardwoods/Upland Conifer	8		Glacial Lake Algonquin Aspen to N. Hardwoods	13	53
Glacial Lake Algonquin	Upland Conifer	13	7, 39	Glacial Lake Algonquin Aspen to Upland Conifer	14	45
Glacial Lake Algonquin	Aspen to Upland Conifer	85		Glacial Lake Algonquin Aspen to Upland Conifer	14	47
Glacial Lake Algonquin	aspen to northern red oak-red maple	6	20	Glacial Lake Algonquin Aspen to Oak	15	41
Glacial Lake Algonquin	Oak	23		Glacial Lake Algonquin Aspen to Oak	15	42
Glacial Lake Algonquin	aspen to northern red oak-upland conifer	15		Glacial Lake Algonquin Aspen to Oak	15	54
Low Low Outwash	Upland Conifer	44	10,9	Low Outwash Lowland Conifer	16	17
Low Low Outwash	aspen to northern red oak-red maple	1		Low Outwash Aspen to Lowland Conifer	17	18
Low Low Outwash	aspen to northern red oak-upland conifer	1		Low Outwash Aspen to Lowland Conifer	17	19
Low Low	Aspen to N. Hardwoods	16		Low Outwash Aspen to	17	20

Outwash				Lowland Conifer		
Low Low Outwash	Aspen to Upland Conifer	49	17	Low Outwash Aspen to Lowland Conifer	17	24
Low Low Outwash	Aspen to N. Hardwoods/Upland Conifer	5		Low Outwash Aspen to Lowland Conifer	17	25
Moraine	Colonial Point	120	37	Indian Point Reserve	18	77
Moraine/GLA	Thinned Hardwoods	236	18	Thinned Hardwoods	19	88
High Outwash/GLA	ExPlantation	567	15, 35, 21, 8, 19	Former Plantation	20	99
Shores&IceContact	Open	13		Open	21	10
Low Outwash	Open	154		Open	21	13
Low Low Outwash	Open	1		Open	21	16
High Outwash	Open	28		Open	21	33
Moraine	Open	33		Open	21	39
Glacial Lake Algonquin	Open	29		Open	21	46

APPENDIX TABLE B. Given are LANDIS-II/PnET species parameterization values and their sources.

	Common name	**PnET name**	**FolN**	**SLWmax**	**SLWDel**	**TOfol**	**AmaxA**	**HalfSat**
Units	n/a	n/a	%(mg/g)	g/m2	g-1fol	proportion/yr	nmol CO2 g-1 leaf s-1	µmol/m2/sec
Valid range	n/a	n/a	0<N<10	0<N<1000	0<N<2	0<N<1	-500< N <+500	int > 0
	Balsam fir	abiebals	1.1[a]	198.33[h]	0[k,l]	0.111[m]	5.3 [k,l]	125[n]
	Red maple	acerrubr	2.0[b]	79[i]	0.2 [k,l]	1	-46 [k,l]	150.33[o]
	Sugar maple	acersacc	1.8[c]	58.17[i]	0.2 [k,l]	1	-46 [k,l]	100.33[o]
	Paper birch	betupapy	1.91[c]	64.8[j]	0.2 [k,l]	1	-46 [k,l]	200[n]
	Shagbark Hickory	caryovat	2.2	60	0.2	1	-46	150
	American beech	fagugran	1.9[b]	63[i]	0.2 [k,l]	1	-46 [k,l]	130[p]
	White ash	fraxamer	2.13[d]	77.3[h]	0.2 [k,l]	1	-46 [k,l]	200[q]
	White spruce	piceglau	0.99[e]	282.185[h]	0 [k,l]	0.118[m]	5.3 [k,l]	200[n]
	Red pine	pinuresi	1.28[r]	267.26[h]	0 [k,l]	0.222[m]	5.3 [k,l]	230[r]
	White pine	pinustro	1.7[d]	143.27[j]	0 [k,l]	0.5[m]	5.3 [k,l]	210[s]
	Bigtooth aspen	popugran	2.8[b]	76[i]	0.2 [k,l]	1	-46 [k,l]	250[t]
	Trembling aspen	poputrem	2.61[c]	99[i]	0.2 [k,l]	1	-46 [k,l]	250[t]
	Northern red oak	querrubr	2[b]	65.52[j]	0.2 [k,l]	1	-46 [k,l]	185[o]
	American basswood	tiliamer	2.61[g]	60.81[h]	0.2 [k,l]	1	-46 [k,l]	130[q]
	Eastern hemlock	tsugcana	0.99[f]	122.55[h]	0 [k,l]	0.3333[m]	5.3 [k,l]	82.815[p]

Variable	**Common name**	**PnET name**	**PsnTMin**	**PsnTOpt**	**k**	**FracFol**	**H3**	**H4**
Units	n/a	n/a	°C	°C	none	proportion/yr	m pressure head	m pressure head
Valid range	n/a	n/a	decimal > 0.0	decimal > 0.0	0<dec. <1.0	0.0< decimal <1.0	absolute value	absolute value
	Balsam fir	abiebals	2[v]	19[v]	0.5 [k,l]	0.1 [v]	114 [u]	147[u]
	Red maple	acerrubr	4 [v]	20[w]	0.58 [k,l]	0.02 [v]	131 [u]	154[u]
	Sugar maple	acersacc	2 [v]	20[w]	0.58 [k,l]	0.02 [v]	114 [u]	147[u]
	Paper birch	betupapy	3 [v]	24[w]	0.58 [k,l]	0.02 [v]	100 [u]	140 [u]

			2	25	0.58	0.02	111	147
	American beech	fagugran	2[v]	19[w]	0.58[k,l]	0.02[v]	114[u]	147[u]
	White Ash	fraxamer	3[v]	20[w]	0.58[k,l]	0.02[v]	131[u]	154[u]
	White spruce	piceglau	2[v]	20[v]	0.5[k,l]	0.1[v]	131[u]	154[u]
	Red pine	pinuresi	3[v]	21[v]	0.5[k,l]	0.1[v]	150[u]	160[u]
	White pine	pinustro	3[v]	20[x]	0.5[k,l]	0.1[v]	150[u]	160[u]
	Bigtooth Aspen	popugran	2[v]	25[w]	0.58[k,l]	0.02[v]	100[u]	140[u]
	Trembling aspen	poputrem	2[v]	22[v]	0.58[k,l]	0.02[v]	100[u]	140[u]
	Northern red oak	querrubr	2[v]	22[w]	0.58[k,l]	0.02[v]	131[u]	154[u]
	American basswood	tiliamer	3[v]	23[w]	0.58[k,l]	0.02[v]	131[u]	154[u]
	Eastern hemlock	tsugcana	3[v]	21[v]	0.5[k,l]	0.1[v]	114[u]	147[u]

APPENDIX TABLE C. Sources of parameter values used in the LANDIS-II/PnET parameterization.

Appendix Table A superscript reference/s	**Source Citation**
a	Yin, X. (1993). Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Canadian Journal of Forest Research*, *23*(8), 1587–1602.
b	Value calibrated to match UMBS output
c	Bergen, K. M., & Dronova, I. (2007). Observing succession on aspen-dominated landscapes using a remote sensing-ecosystem approach. *Landscape Ecology*, *22*(9), 1395–1411.
d	Reich, P. B., Walters, M. B., Kloeppel, B. D., & Ellsworth, D. S. (1995). Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia*, *104*(1), 24–30.
e	Perala, D. A., & Alban, D. H. (1982). Biomass, nutrient distribution and litterfall in Populus, Pinus and Picea stands on two different soils in Minnesota. *Plant and Soil*, *64*(2), 177–192.
f	Reich, P. B., Walters, M. B., Ellsworth, D. S., Vose, J. M., Volin, J. C., Gresham, C., & Bowman, W. D. (1998). Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, *114*, 471-482.

g	Martin, M. E., & Aber, J. D. (1997). High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. *Ecological Applications*, *7*(2), 431–443.
h	Chiang, J. M. (2007). *Aboveground carbon storage and net primary production in human impacted forests under current and future climate scenarios* (Doctoral dissertation, Ohio University).
i	Jurik, T. W. (1986). Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *American Journal of Botany*, *73*(8), 1083–1092.
j	Bryan, A. M., Cheng, S. J., Ashworth, K., Guenther, A. B., Hardiman, B. S., Bohrer, G., & Steiner, A. L. (2015). Forest-atmosphere BVOC exchange in diverse and structurally complex canopies: 1-D modeling of a mid-successional forest in northern Michigan. *Atmospheric Environment*, *120*, 217–226.
k	Aber, J. D., Ollinger, S. V., Federer, C. A., Reich, P. B., Goulden, M. L., Kicklighter, D. W., Melillo, J. M., & Lathrop, R. G. (1995). Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research*, *5*(3), 207–222.
l	Ollinger, S. V., & Smith, M.-L. (2005). Net primary production and canopy nitrogen in a temperate forest landscape: an analysis using imaging spectroscopy, modeling and field data. *Ecosystems*, *8*(7), 760–778.
m	Barnes, B. V., & Wagner, W. H. (2004). Michigan trees: a guide to the trees of the Great Lakes region. University of Michigan Press. Reciprocal of leaf longevity, if a range was given the midpoint was used.
n	Landhäusser, S. M., & Lieffers, V. J. (2001). Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. *Tree Physiology*, *21*(4), 243–250.
o	Ryu, S.-R., Chen, J., Noormets, A., Bresee, M. K., & Ollinger, S. V. (2008). Comparisons between PnET-Day and eddy covariance based gross ecosystem production in two Northern Wisconsin forests. *Agricultural and Forest Meteorology*, *148*(2), 247–256.
p	Madison, C. (2018). *The Photosynthesis-Foliar Nitrogen Relationship in Decidous and Evergreen Forest of New Hampshire* (Doctoral dissertation, University of New Hampshire).
q	Bazzaz, F. A., & Carlson, R. W. (1982). Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia*, *54*(3), 313–316.
r	Calculated from *Pinus strobus* and *Pinus banksiana* values
s	Maier, C. A., & Teskey, R. O. (1992). Internal and external control of net photosynthesis and stomatal conductance of mature eastern white pine (Pinus strobus). *Canadian Journal of Forest Research*, *22*(9), 1387–1394.
t	Jurik, T. W., Weber, J. A., & Gates, D. M. (1984). Short-term effects of CO2 on gas exchange of leaves of bigtooth aspen (Populus grandidentata) in the Field. *Plant Physiology*, *75*(4), 1022–1026.
u	Pers. Comm. With Eric Gustafson

v	Gustafson, E. J., de Bruijn, A., Lichti, N., Jacobs, D. F., Sturtevant, B. R., Foster, J., Miranda, B. R., & Dalgleish, H. J. (2017). The implications of American chestnut reintroduction on landscape dynamics and carbon storage. *Ecosphere, 8*(4), e01773.
w	Jurik, T. W., Weber, J. A., & Gates, D. M. (1988). Effects of temperature and light on photosynthesis of dominant species of a northern hardwood forest. *Botanical Gazette*, *149*(2), 203–208.
x	Jurik, T. W., Briggs, G. M., & Gates, D. M. (1988). Springtime recovery of photosynthetic activity of white pine in Michigan. *Canadian Journal of Botany, 66*(1), 138–141.
y	PNet/LANDIS-II guide

APPENDIX TABLE D. Given are generic LANDIS-II species parameterization values and their sources.

Variable	Common Name		Longevity	Sexual Maturity	Effective Seed Dispersal Distance	Maximum Seed Dispersal Distance	Vegetative Reprod. Prob	Sprout Age Min	Sprout Age Max
Units			years	years	m	m	N/A	years	years
Valid Range			Integer> 0	0 < integer ≤ Longevity	0 < N ≤ Max Seed Dist.	integer > 0.	0.0 ≤ number ≤ 1.0	0 < integer ≤ Longevity.	Min Sprout Age ≤ N ≤ Longevity.
	Balsam fir	abiebals	200[a]	25[c,e]	60[e]	160[e]	0[e]	0	0
	Red maple	acerrubr	170[b]	4[c]	100[e]	200[e]	0.5[e]	20[i]	100[e]
	Sugar maple	acersacc	400[c]	22[c]	50[e]	330[e]	0.3[e]	20[i]	100[e]
	Paper birch	betupapy	110[b]	15[c]	60[e]	5,000[e]	0.8[e]	20[i]	100[b]
	Shagbark Hickory	caryovat	300[c]	40[c]	30[g]	5,000[h]	0.5[c]	20[i]	70[c]
	American beech	fagugran	300[c]	40[c]	30[c]	5,000[h]	0.8[c]	20[i]	100[c]
	White ash	fraxamer	280[d]	20[c]	70[e]	140[e]	0.3[e]	20[i]	100[e]
	White spruce	piceglau	300[c]	30[c]	27[e]	300[e]	0[e]	0	0
	Red pine	pinuresi	350[c]	15[c,e]	12[e]	300[e]	0[e]	0	0

	White pine	pinustro	400[c]	20[c,e]	60[e]	210[e]	0[e]	0	0
	Bigtooth aspen	popugran	120[b]	10[c]	500[e]	5,000[e]	0.9[e]	20[i]	70[e]
	Trembling aspen	poputrem	110[b]	10[c]	500[e]	5,000[e]	0.9[e]	20[i]	60[e]
	Northern red oak	querrubr	300[d]	25[c]	3[e]	5,000[e]	0.5[e]	20[i]	45[e]
	American basswood	tiliamer	200[c]	10[c]	20[e]	80[e]	0.7[c]	20[i]	110[e]
	Eastern hemlock	tsugcana	800[c]	30[f]	20[c]	53[c]	0[c]	0	0

APPENDIX TABLE E. Sources of parameter values used in the LANDIS-II parameterization.

Appendix Table D superscript reference/s	**Source Citation**
a	Uchytil, R. J. (1991). Abies balsamea. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Accessed 3/30/2020 at: https://www.fs.fed.us/database/feis/plants/tree/abibal/all.html
b	Derived from field data
c	Burns, R. M., & Honkala, B. H., [Technical coordinators] (1990). Silvics of North America: Volume 1. Conifers; Volume 2. Hardwoods. *United States Department of Agriculture (USDA), Forest Service, Agriculture Handbook*, *654*. https://www.fs.usda.gov/treesearch/pubs/1548
d	Loehle, C. (1988). Tree life history strategies: The role of defenses. *Canadian Journal of Forest Research*, 18(2), 209–222.
e	Lucash, M. S., Scheller, R. M., Sturtevant, B. R., Gustafson, E. J., Kretchun, A. M., & Foster, J. R. (2018). More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change. *Ecosphere, 9*(6), 22.
f	Carey, J. H. (1993). Tsuga canadensis. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Accessed 4/2/2020 at https://www.fs.fed.us/database/feis/plants/tree/tsucan/all.html
g	Tirmenstein, D. A. (1991). Carya ovata. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Accessed 4/2/2020 at https://www.fs.fed.us/database/feis/plants/tree/carova/all.html
h	Darley-Hill, S., & Johnson, W. C. (1981). Acorn dispersal by the blue jay (Cyanocitta cristata). *Oecologia, 50*(2), 231–232.
i	Pers. Comm with Eric Gustafson

APPENDIX TABLE F. Given are the parameterizations across species for LANDIS-II PNET extension

PnETGenericParameters	Value	Units	Valid Range
MaxCanopyLayers	2[a]	NA	NA
MaxDevLyrAv	8000[a]	NA	NA
IMAX	5[a]	NA	NA
BFolResp	0.1[a]	proportion.	0.0< decimal <1.0
MaintResp	0.002[a]	proportion of NSC lost per month.	0.0< decimal <1.0
DNSC	0.05[a]	proportion of active biomass.	0.0< decimal <1.0.
FracBelowG	0.33[a]	proportion	0.0< decimal <1.0.
PrecipEvents	11[a]	count	decimal >1.0.
PreventEstablishment	TRUE[a]	NA	TRUE or FALSE
Wythers	TRUE[a]	NA	TRUE or FALSE
DTEMP	TRUE[a]	NA	TRUE or FALSE
CO2AmaxBeff	1[a]	NA	NA
PSNAgeRed	5[a]	Proportion/yr	TRUE or FALSE
FrActWd	0.00004[a]	0.0<N<0.4	NA

APPENDIX TABLE G. Sources of parameter values used in the LANDIS-II parameterization.

Appendix Table E superscript reference/s	**Source Citation**
a	Default PNET/LANDIS parameters used

APPENDIX TABLE H. Given are the ecoregion parameterization values.

	LandisData	EcoregionParameters								
						soil type				
	Ecoregion Name	RootingDepth	LeakageFrac	PrecLossFrac	SnowSublimFrac	Sand	clay	pctOM	densFactor	gravel
Units	NA	mm								
Valid Range	NA	0<N<1000				0.0<N<1	0.0<N<1	0.0<N<100		0.0<N<1
	LowOutwash	875^{a}	1^{b}	0^{b}	0.15^{b}	0.82^{c}	0.04^{c}	0.93^{c}	1^{b}	0.12^{c}
	HighOutwash	657^{a}	1^{b}	0.5^{c}	0.15^{b}	0.9^{c}	0.02^{c}	0.81^{c}	1^{b}	0.05^{c}
	GlaLakeAlgon	1000^{a}	1^{b}	0^{b}	0.15^{b}	0.89^{c}	0.04^{c}	2.92^{c}	1^{b}	0.06^{c}
	IceContact	1000^{a}	1^{b}	0^{b}	0.15^{b}	0.08^{c}	0.47^{c}	3.59^{c}	1^{b}	0^{c}
	Moraine	1000^{a}	1^{b}	0^{b}	0.15^{b}	0.08^{c}	0.47^{c}	3.59^{c}	1^{b}	0^{c}

APPENDIX TABLE I. Given are the sources of the ecoregion parameterization values.

Appendix Table G superscript	**Source Citation**

reference/s	
a	Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database for Cheboygan and Emmett Counties, MI. Available online. Accessed 2/4/2019 https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx
b	Default Landis-II values used
c	Calibrated to reflect landform productivity. May not reflect actual SSURGO values

APPENDIX TABLE J: This table lists the mean and standard deviation for diameter at breast height and age and the number of trees sampled for each measurement for each species found in each region.

Landform	**Species**	**Mean DBH**	**Std Dev DBH**	**N Trees Measured**	**Mean Age**	**Std Dev Age**	**N Trees Cored**
Low Outwash	BalsamFir	13.26596	6.023551	47	31.85714	15.91046	7
Indian Point Reserve	RedMaple	46.15	15.34422	2	152	18.38478	2
Glacial Lake Algonquin	RedMaple	13.35238	5.906435	42	77.53846	17.73704	13
High Outwash	RedMaple	17.98214	6.303794	28	88.9	9.65459	10
Ice Contact	RedMaple	18.73444	8.152578	45	92.66667	9.785193	9
Low Outwash	RedMaple	13.23529	8.234848	51	53.41667	19.52368	12
Moraine	RedMaple	19.02667	10.21617	45	77.5625	20.92835	16
Indian Point Reserve	SugarMaple	17.4	6.363961	2	78	11.31371	2
High Outwash	SugarMaple	12.05	2.946184	8	62.33333	34.29772	3

Ice Contact	SugarMaple	16.68	5.678053	15	63.33333	13.61372	3
Moraine	SugarMaple	13.29677	8.119496	62	66.53846	17.93793	13
High Outwash	PaperBirch	20.74	4.645751	5	89	8.831761	4
Low Outwash	PaperBirch	15.66667	4.855152	9	83.5	14.0594	4
Indian Point	AmericanBeech	18.425	19.64917	6	80	36.04164	3
Glacial Lake Algonquin	AmericanBeech	6.073913	6.48272	23	60.5	14.84924	2
High Outwash	AmericanBeech	12.78056	6.645369	18	86.33333	13.61372	3
Ice Contact	AmericanBeech	10.55645	8.268703	31	62.42857	25.36965	7
Moraine	AmericanBeech	10.41343	9.670678	70	82	16.3596	12
Ice Contact	WhiteAsh	20.45	1.202082	2	100	NA	1
Low Outwash	WhiteAsh	12.5	1.555635	2	29	NA	1
Low Outwash	WhiteSpruce	17.44815	5.25184	27	43.88889	18.85765	9
Glacial Lake Algonquin	RedPine	19.21905	10.02257	63	58.53846	13.72112	13
High Outwash	RedPine	16.97407	4.770469	27	67	2.645751	3
Low Outwash	RedPine	22.84	15.66559	25	56	23.13315	8
Glacial Lake Algonquin	WhitePine	8.631846	7.679757	65	42.47059	20.08456	17
High Outwash	WhitePine	8.807143	9.967004	42	44.55556	24.42904	9
Ice Contact	WhitePine	12.55	6.237209	10	38	8.869423	4
Low Outwash	WhitePine	18.33729	15.94889	59	55.33333	25.76363	18
Moraine	WhitePine	17.2	NA	1	29	NA	1
Glacial Lake	BigtoothAsp	28.80149	6.41198	67	85.625	16.54438	16

Algonquin	en						
High Outwash	BigtoothAspen	25.77879	4.526778	33	87.77778	20.83733	9
Ice Contact	BigtoothAspen	40.385	10.43467	20	88.44444	19.25559	9
Low Outwash	BigtoothAspen	22.2375	9.919199	16	68.09091	25.12152	11
Moraine	BigtoothAspen	33.8266	13.02277	47	81.75	22.66806	12
Low Outwash	TremblingAspen	26.1	10.35857	19	60.09091	18.59814	11
Indian Point Reserve	RedOak	61.38	18.5543	5	150.5	49.0068	4
Glacial Lake Algonquin	RedOak	25.27593	9.575695	54	91.57895	15.62873	19
High Outwash	RedOak	24.68378	10.07269	37	87.23077	27.23097	13
Ice Contact	RedOak	36.575	9.60256	4	93.33333	9.609024	3
Low Outwash	RedOak	12.2875	4.506008	8	25.33333	10.69268	3
Moraine	RedOak	16.02059	15.70622	17	49.55556	22.32214	9
Ice Contact	Basswood	27.45	8.838835	2	71	7.071068	2
Indian Point Reserve	EasternHemlock	27.25	6.29325	2	110.5	3.535534	2
High Outwash	EasternHemlock	39.25	0.494975	2	84	NA	1
Ice Contact	EasternHemlock	11.85	0.212132	2	30	1.414214	2

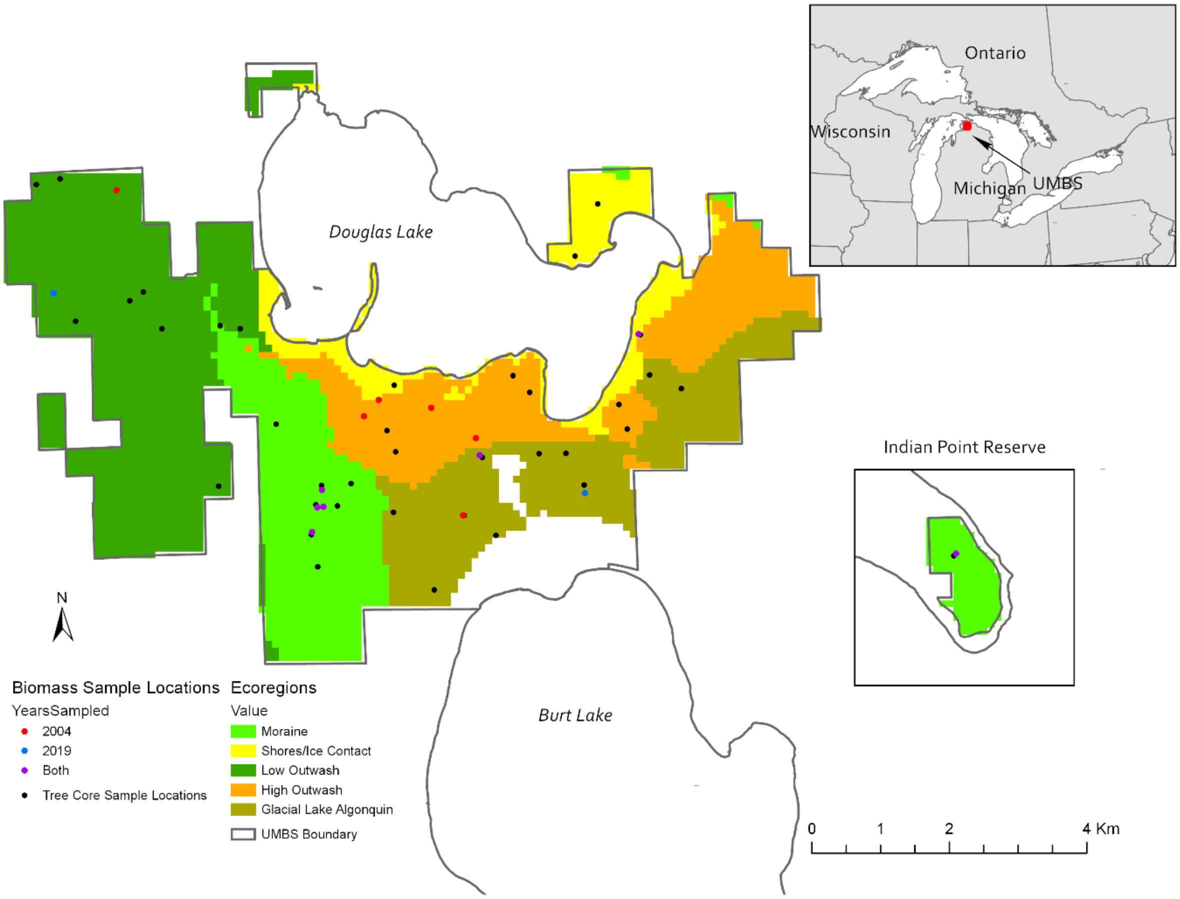
APPENDIX TABLE K: This table lists the mean biomass values for each species on each landform. 2004 biomass values were taken from Bergen and Dronova (2007).

Landform	**Species**	**2004**	**2019**
LowOutwash	BalsamFir	NA	0.37837
Indian Point Reserve	RedMaple	47.41574	38.47186
GlacialLakeAlgonquin	RedMaple	3.652908	23.88092
HighOutwash	RedMaple	10.12073	NA
IceContact	RedMaple	45.9091	56.68441
LowOutwash	RedMaple	0.519595	18.15723
Moraine	RedMaple	25.62567	24.53011
Indian Point Reserve	SugarMaple	59.30068	17.05572
GlacialLakeAlgonquin	SugarMaple	NA	0.556963
IceContact	SugarMaple	1.0857	15.82069
Moraine	SugarMaple	29.32567	52.40608
Indian Point Reserve	PaperBirch	2.070694	NA
GlacialLakeAlgonquin	PaperBirch	NA	0.49095
HighOutwash	PaperBirch	6.529652	NA
LowOutwash	PaperBirch	1.821415	0.40929
Moraine	PaperBirch	0.081965	NA
Indian Point Reserve	AmericanBeech	45.67057	90.75099
GlacialLakeAlgonquin	AmericanBeech	NA	1.09934
HighOutwash	AmericanBeech	2.049428	NA
IceContact	AmericanBeech	27.8221	26.98846
Moraine	AmericanBeech	22.31288	77.4223
Indian Point Reserve	WhiteAsh	9.245887	1.830043

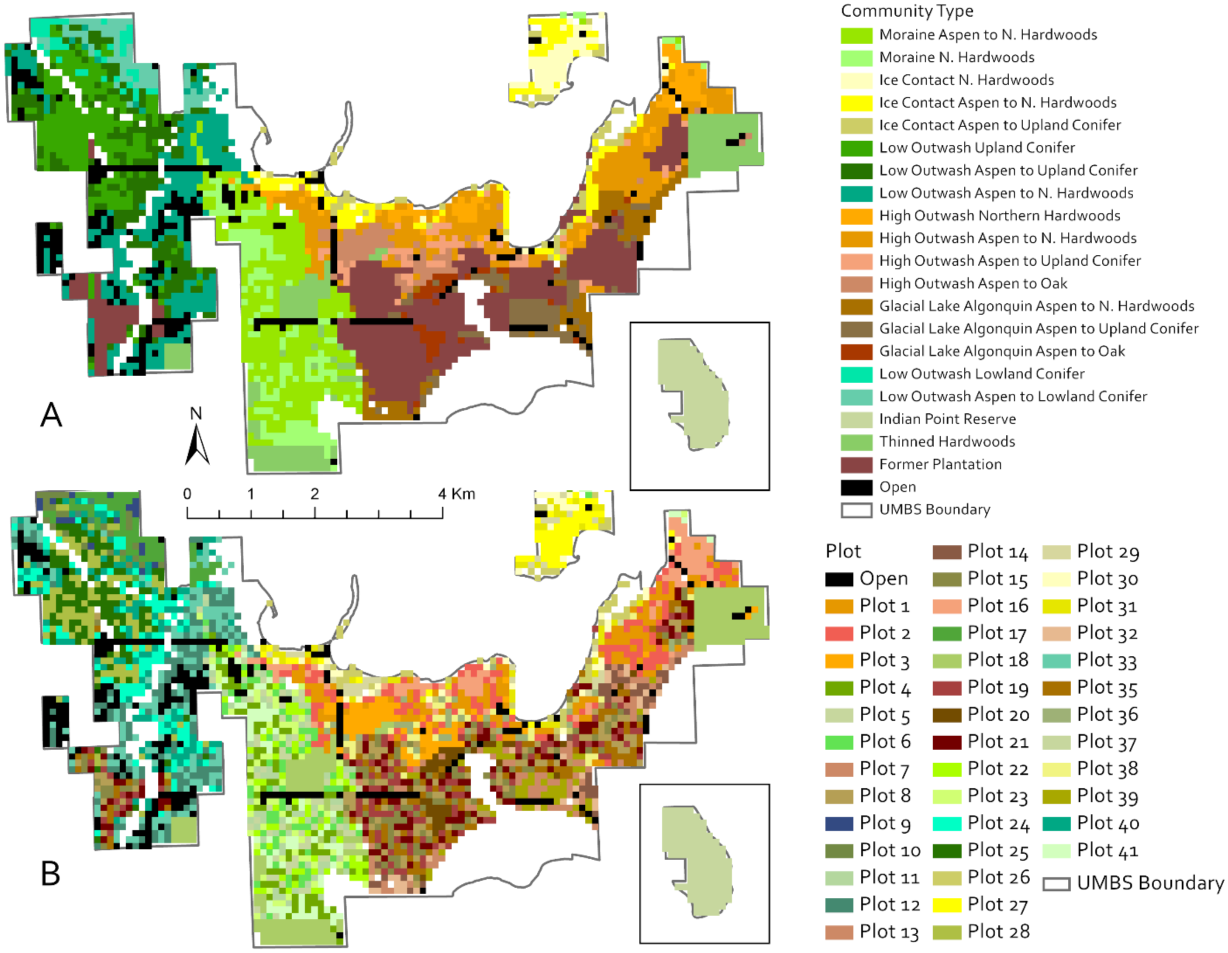
LowOutwash	WhiteSpruce	7.378688	NA
GlacialLakeAlgonquin	RedPine	2.005441	35.63406
HighOutwash	RedPine	7.634635	NA
LowOutwash	RedPine	NA	135.3971
Indian Point Reserve	WhitePine	20.92911	NA
GlacialLakeAlgonquin	WhitePine	5.631737	6.700896
HighOutwash	WhitePine	2.772069	NA
IceContact	WhitePine	NA	0.072664
LowOutwash	WhitePine	7.672376	12.71015
LowOutwash	TremblingAspen	45.11413	NA
Indian Point Reserve	BigtoothAspen	10.17372	NA
GlacialLakeAlgonquin	BigtoothAspen	43.90389	93.75939
HighOutwash	BigtoothAspen	47.90339	NA
IceContact	BigtoothAspen	120.4755	206.3867
LowOutwash	BigtoothAspen	3.858677	NA
Moraine	BigtoothAspen	81.38081	97.91934
Indian Point Reserve	RedOak	83.1976	37.76754
GlacialLakeAlgonquin	RedOak	42.87207	19.21595
HighOutwash	RedOak	34.85003	NA
IceContact	RedOak	10.8174	NA
Moraine	RedOak	4.992013	NA
Indian Point Reserve	Basswood	2.615346	NA

APPENDICES – FIGURES

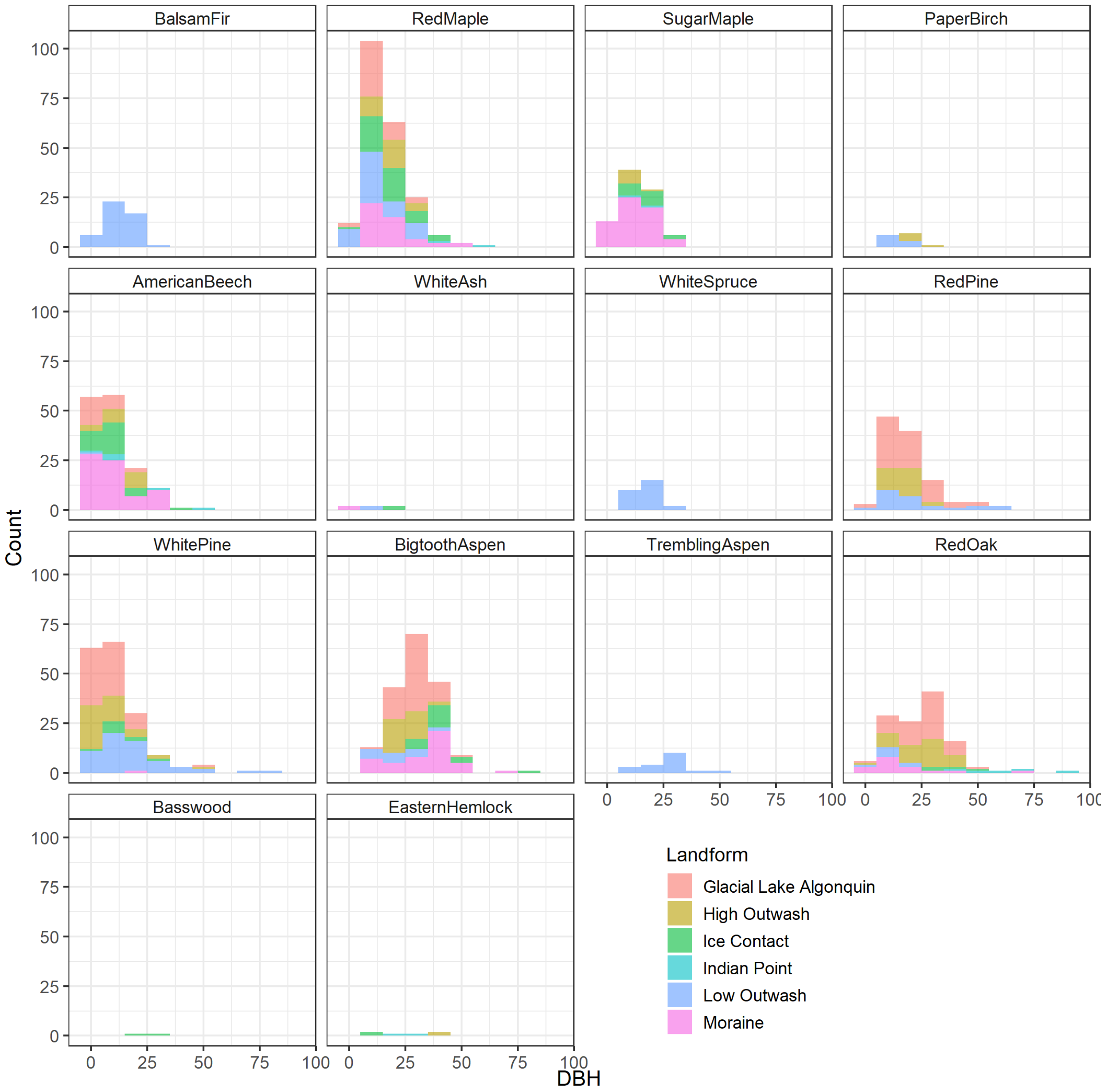
APPENDIX FIGURE A. Shown are the LANDIS-II ecoregions derived from the major landforms of UMBS (main map, Pearsall 1995) plus locations of study field and tree-core plots (circles). Also shown is the location of the UMBS within the upper Great Lakes region (top right inset) and Indian Point Reserve, formerly known as Colonial Point, located south of the main UMBS property by Burt Lake (bottom right inset).



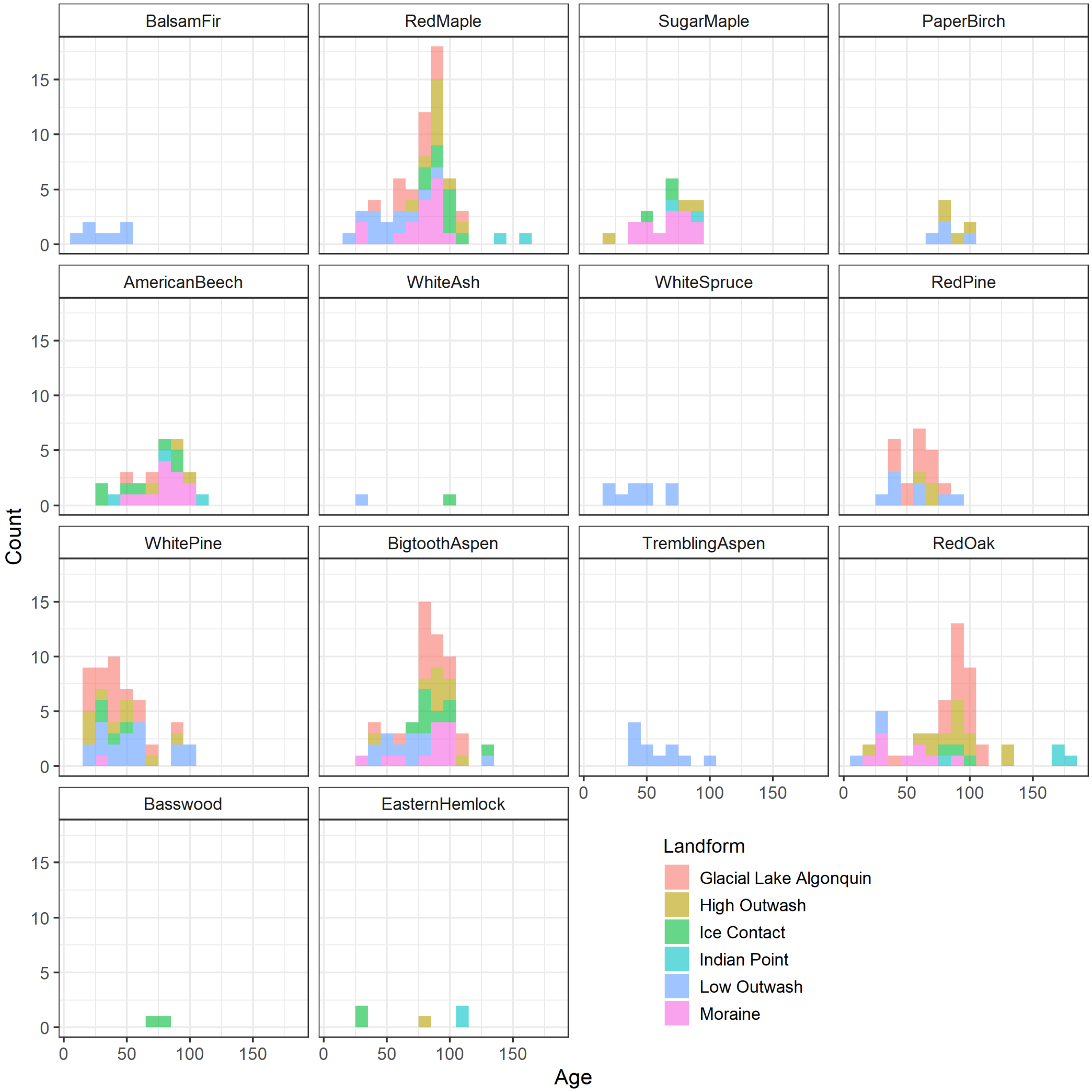
APPENDIX FIGURE B. Shown are the two alternative finalized initial communities rasters (a, b) used as input to the LANDIS-II/PNET model. Initial community raster A combined the field data from sampled plots to create community types. Initial community raster B used the Random Landscape Tool to populate each cell or each community type in initial community raster A with the data of a specific field plot, leading to more heterogeneity.



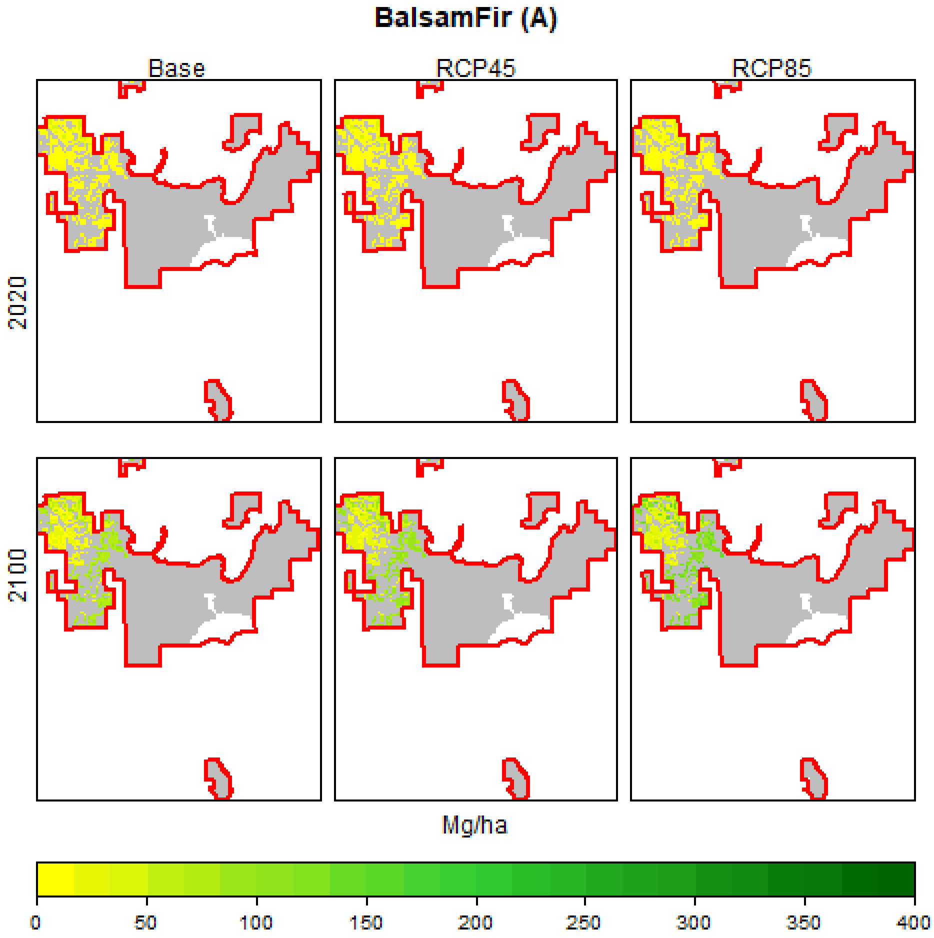
APPENDIX FIGURE D: Shown is a histogram of overstory tree DBH at UMBS, separated by species and LANDIS-II ecoregion (based on Pearsall's (1995) landforms, with Indian Point Reserve separated due to land-use history. All measured trees from the field plots used in analysis are included.

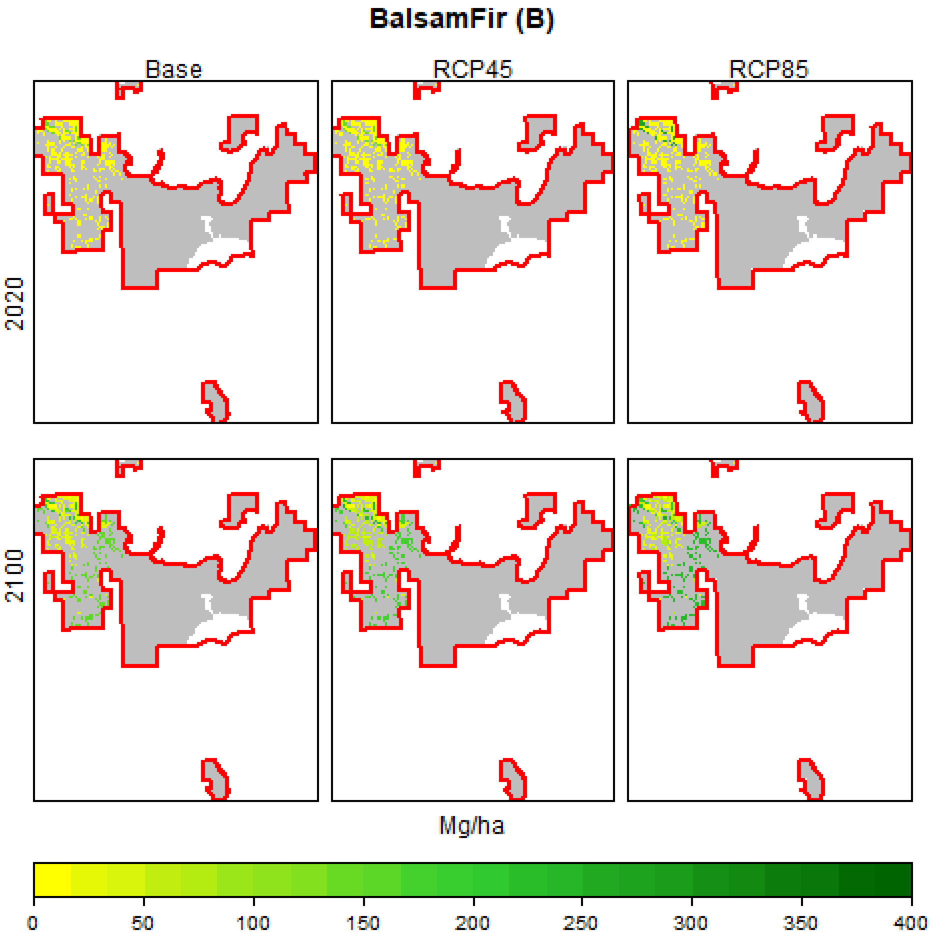

BalsamFir
RedMaple
SugarMaple
PaperBirch
AmericanBeech
WhiteAsh
WhiteSpruce
RedPine
WhitePine
BigtoothAspen
TremblingAspen
RedOak
Basswood
EasternHemlock
Count
100
75
50
25
0
0
25
50
75
100
DBH
Landform
Glacial Lake Algonquin
High Outwash
Ice Contact
Indian Point
Low Outwash
Moraine

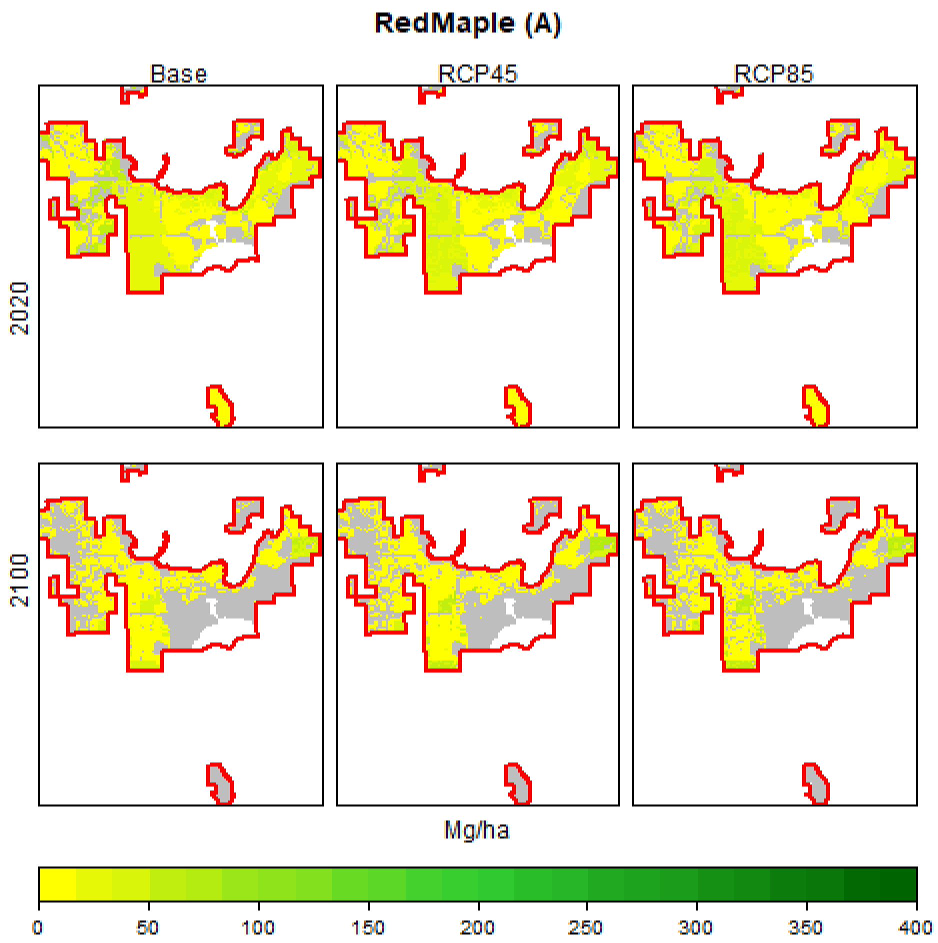
APPENDIX FIGURE E: Shown is a histogram of tree age at UMBS, separated by species and LANDIS-II ecoregion (based on Pearsall's (1995) landforms, with Indian Point Reserve separated due to land-use history. Only the subset of trees measured for age and with readable cores are included.

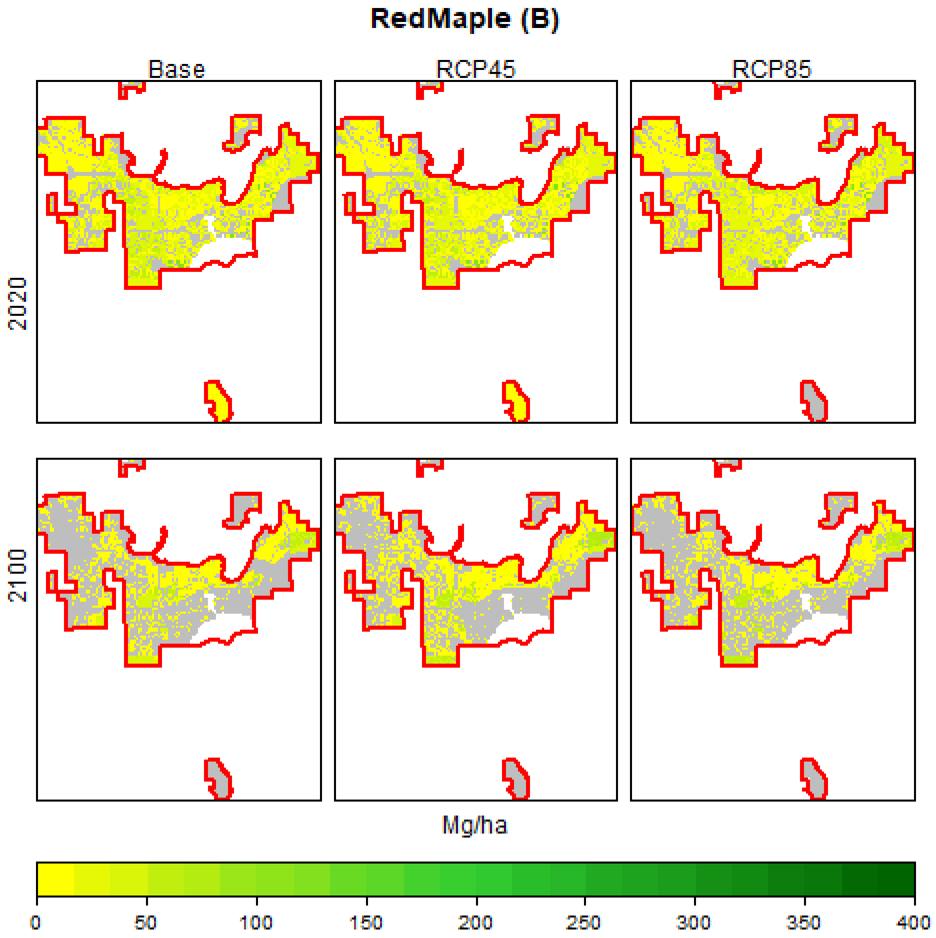


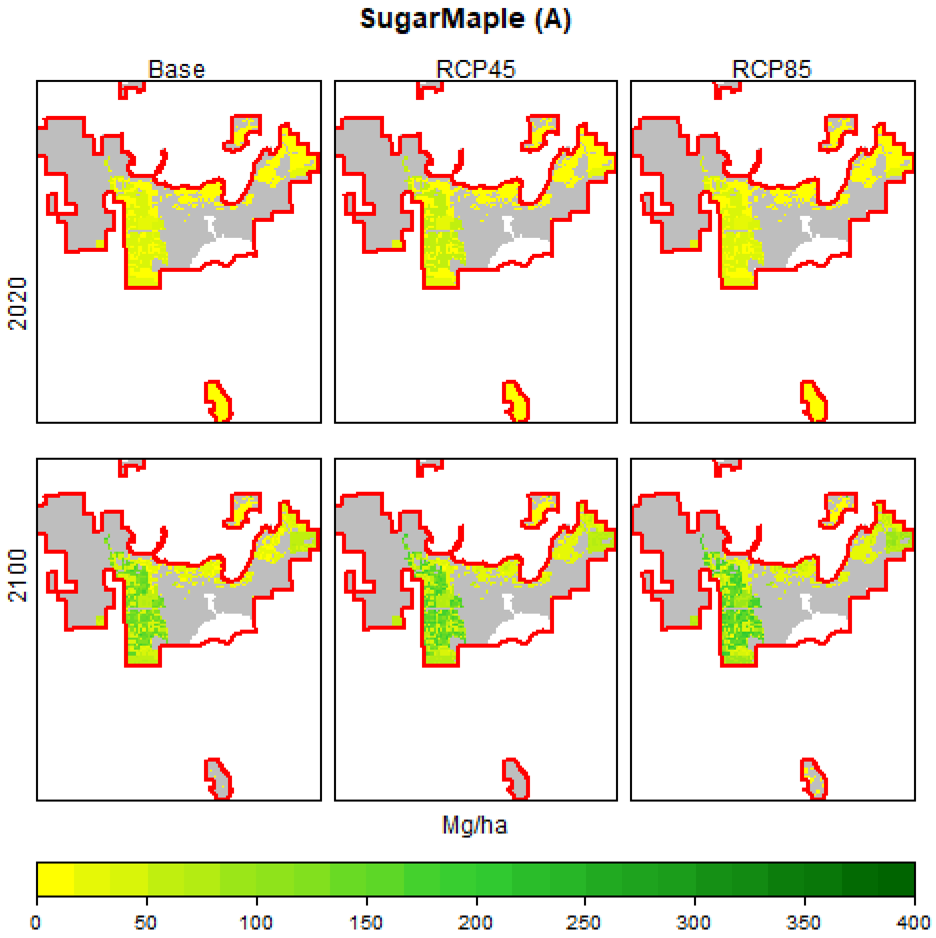
APPENDIX FIGURE F: Given are maps of UMBS showing the distribution of each species biomass upon the landscape at the beginning and end of the model run for three separate climates. Each species has two figures. The first figure, labeled A, displays the results given by using the first input map. The second, labelled B, displays the results given by the second randomly generated input map. The species are listed in alphabetical order for their scientific name. Note that the scale for white pine is different than the rest of the species. The figures given for shagbark hickory come from a separate set of model runs that included it as a species, unlike the other figures.

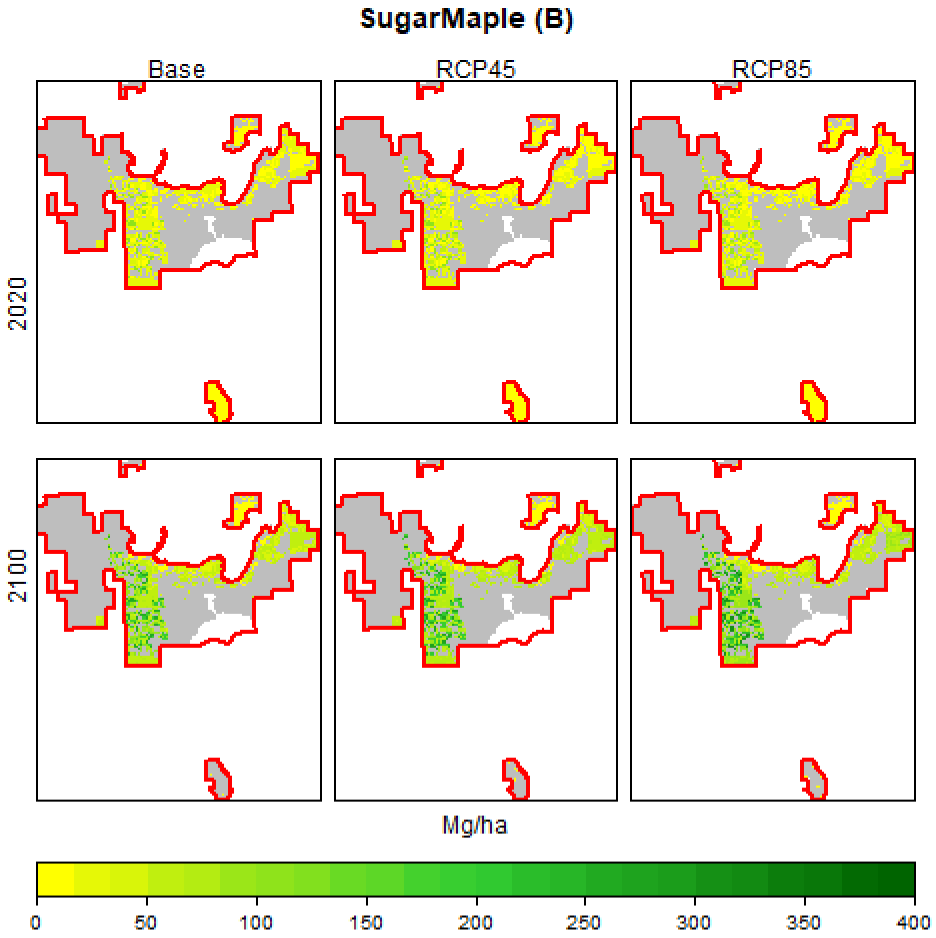


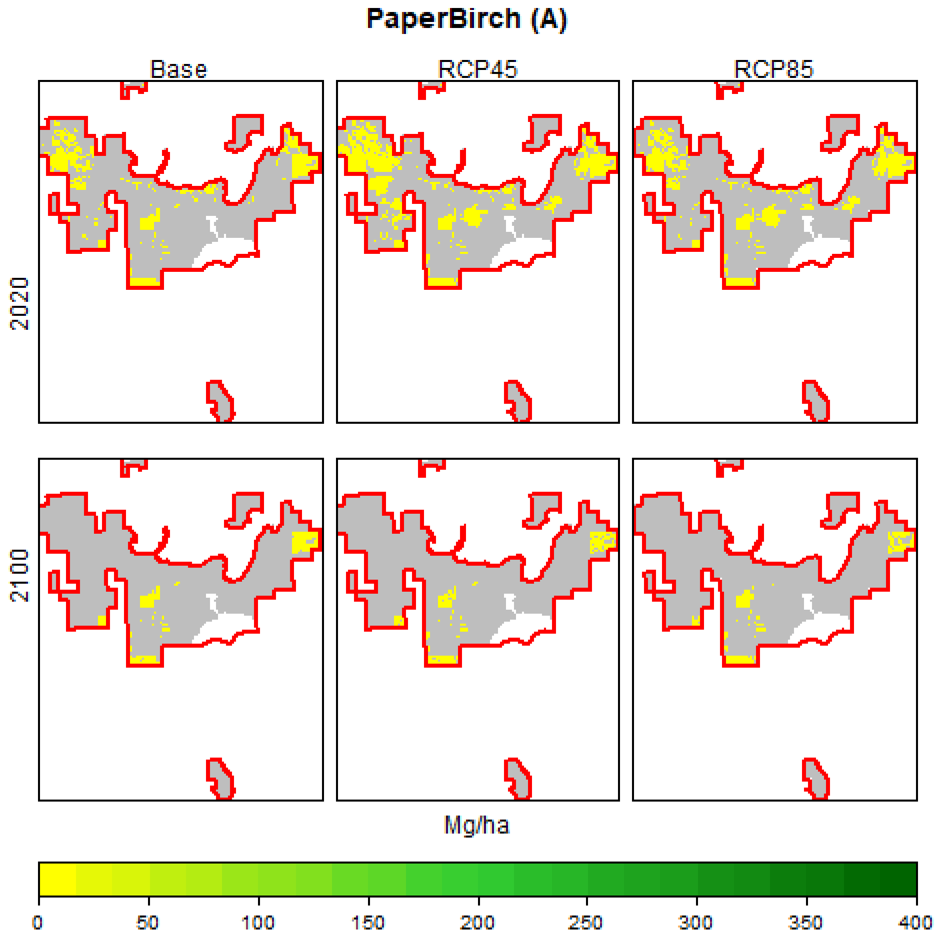

BalsamFir (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

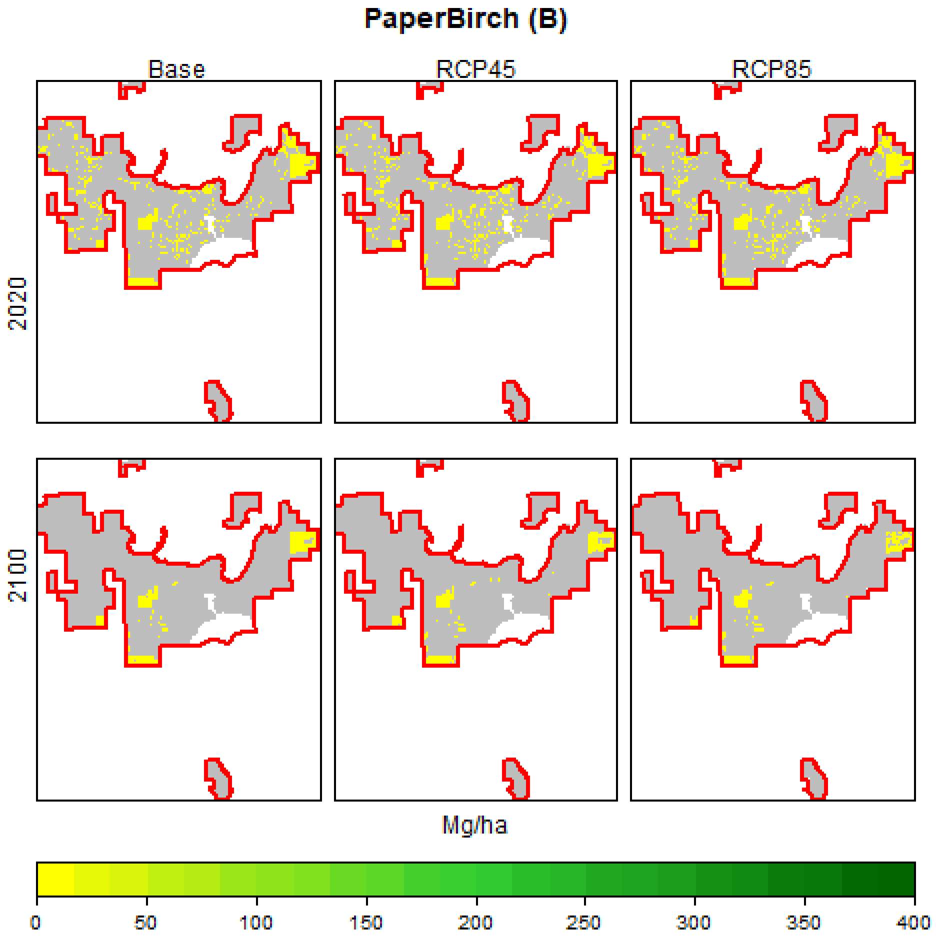

RedMaple (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

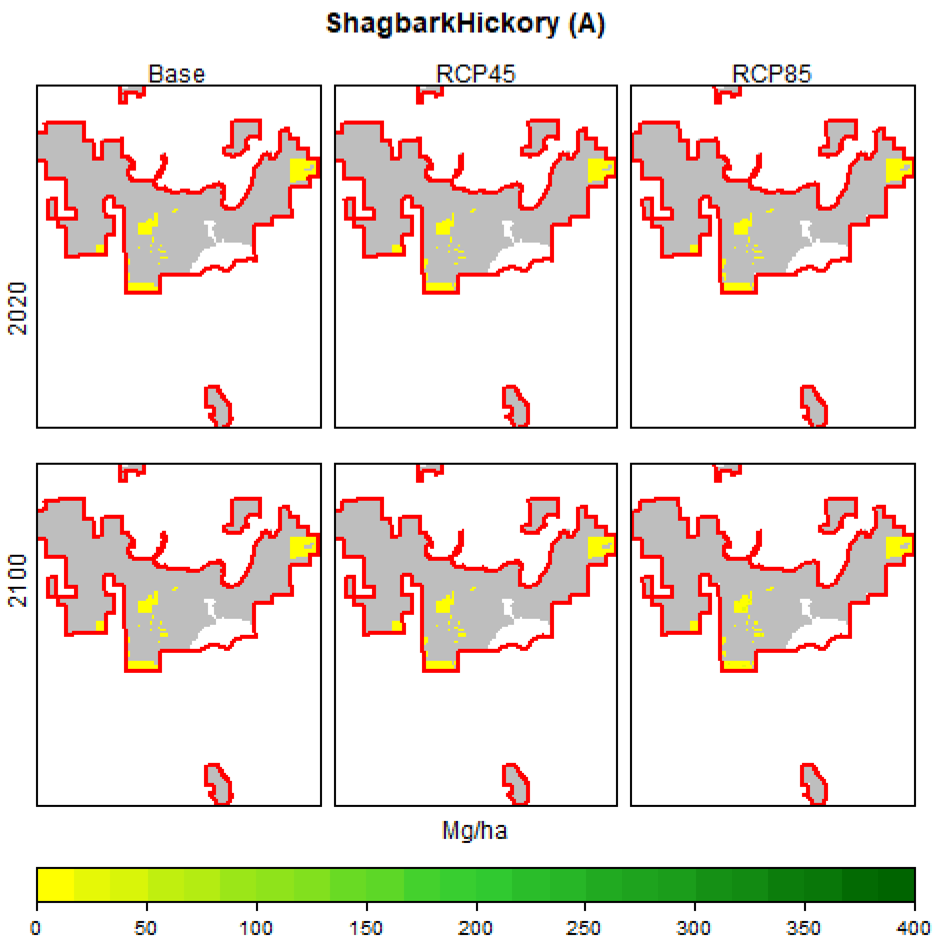

RedMaple (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

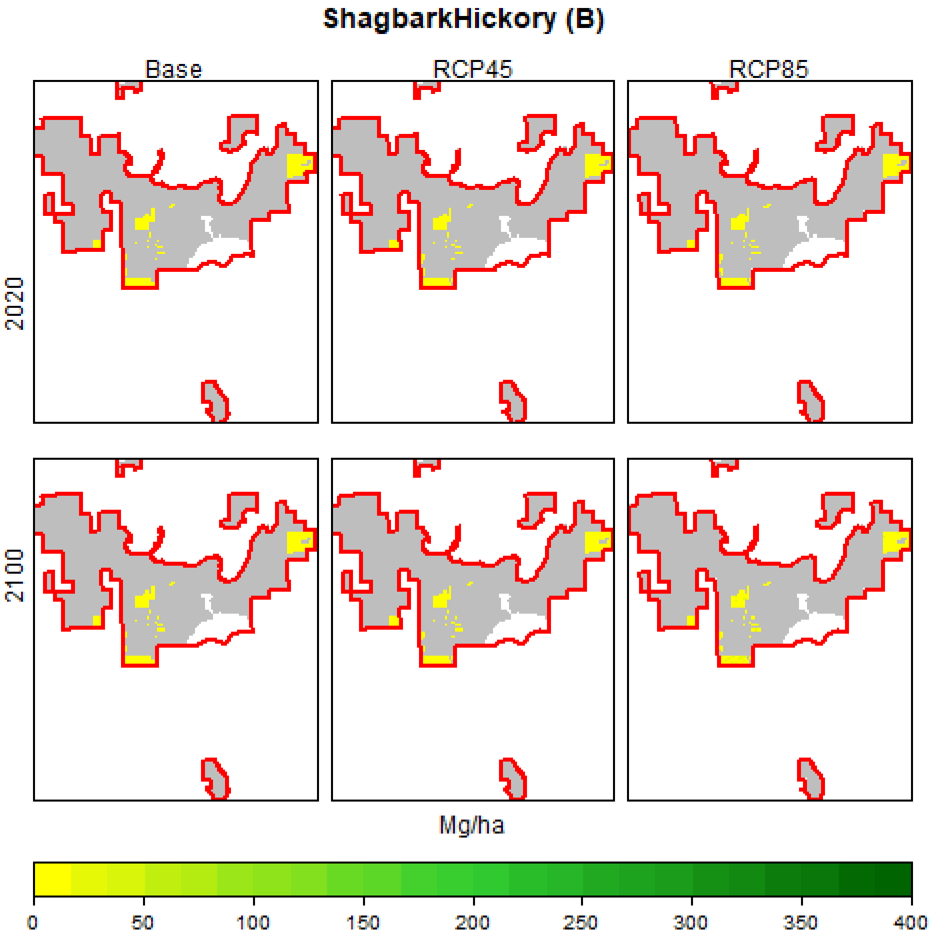

SugarMaple (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

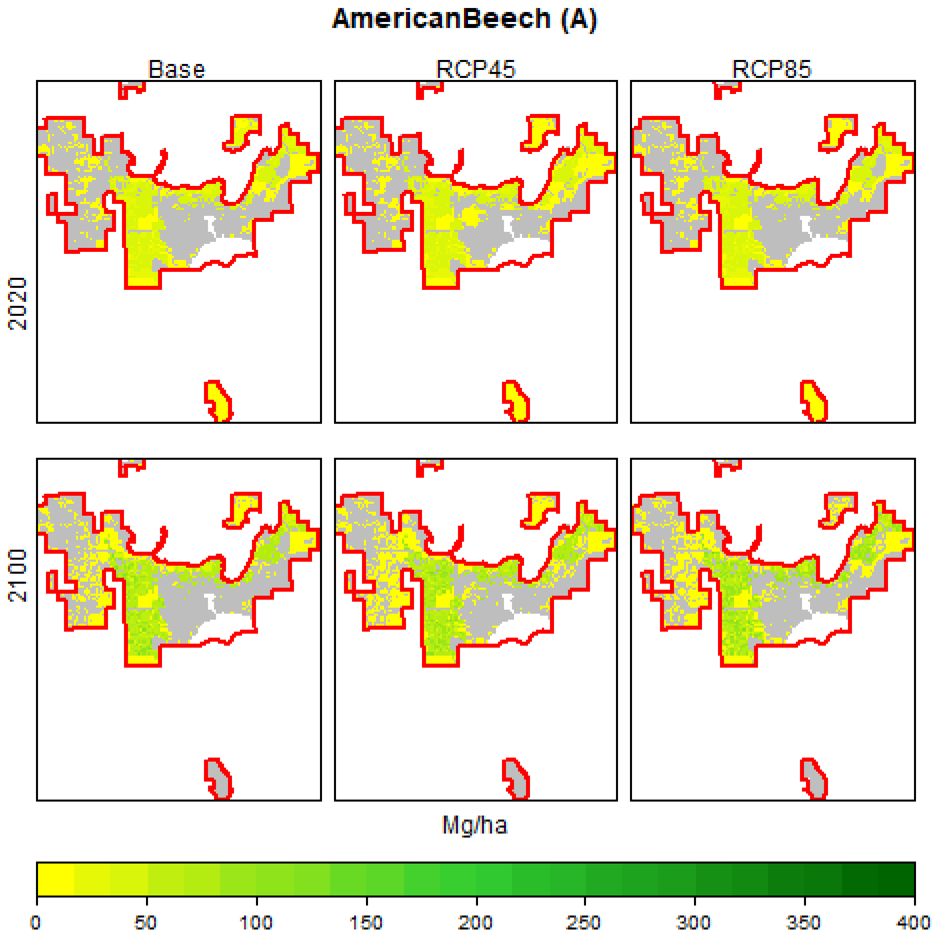

SugarMaple (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

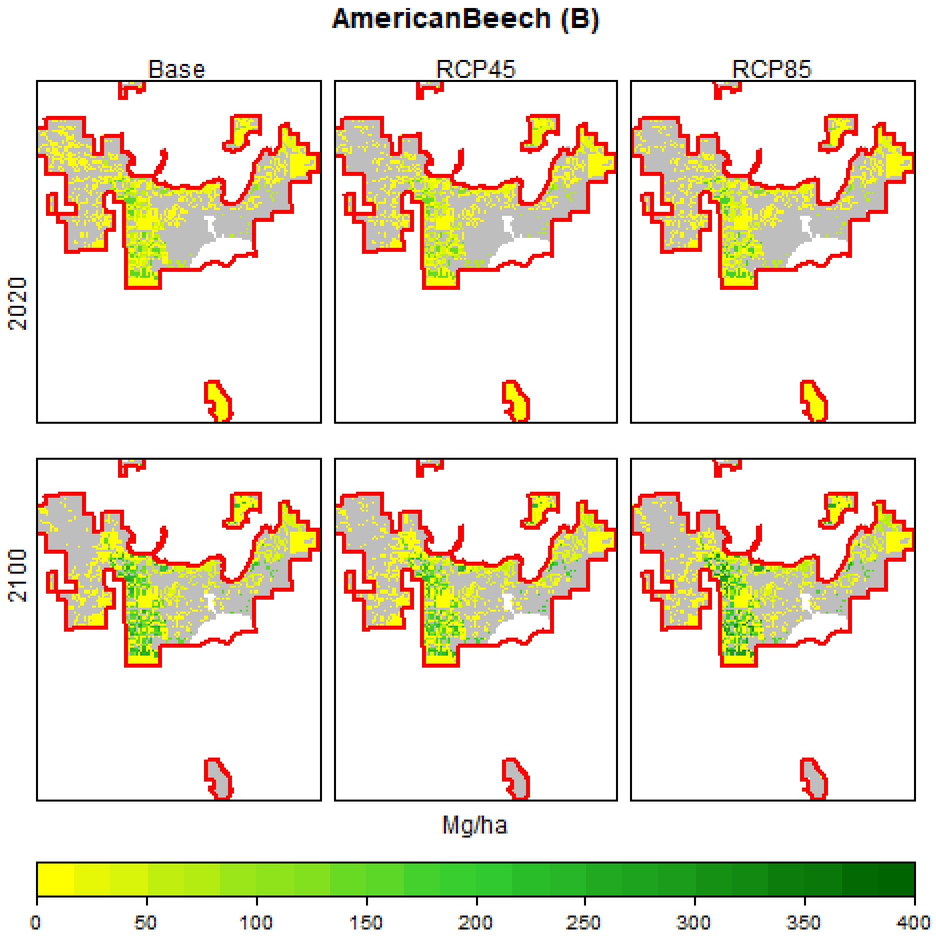

PaperBirch (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

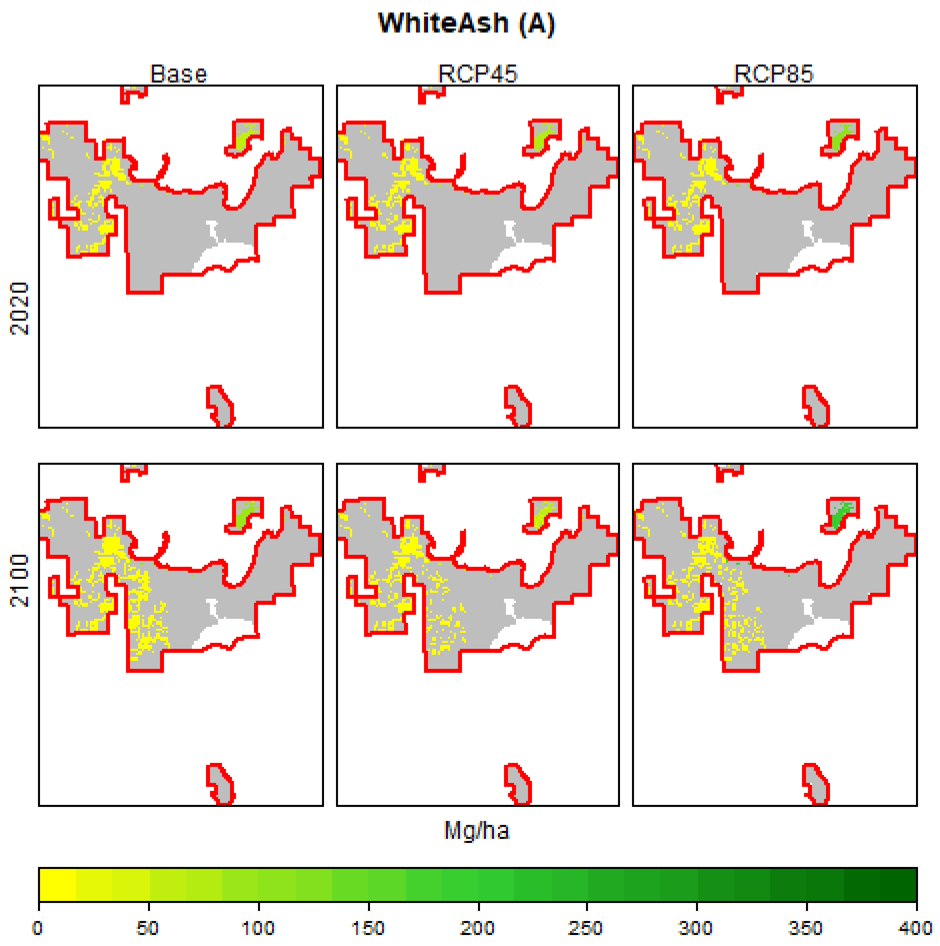

PaperBirch (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

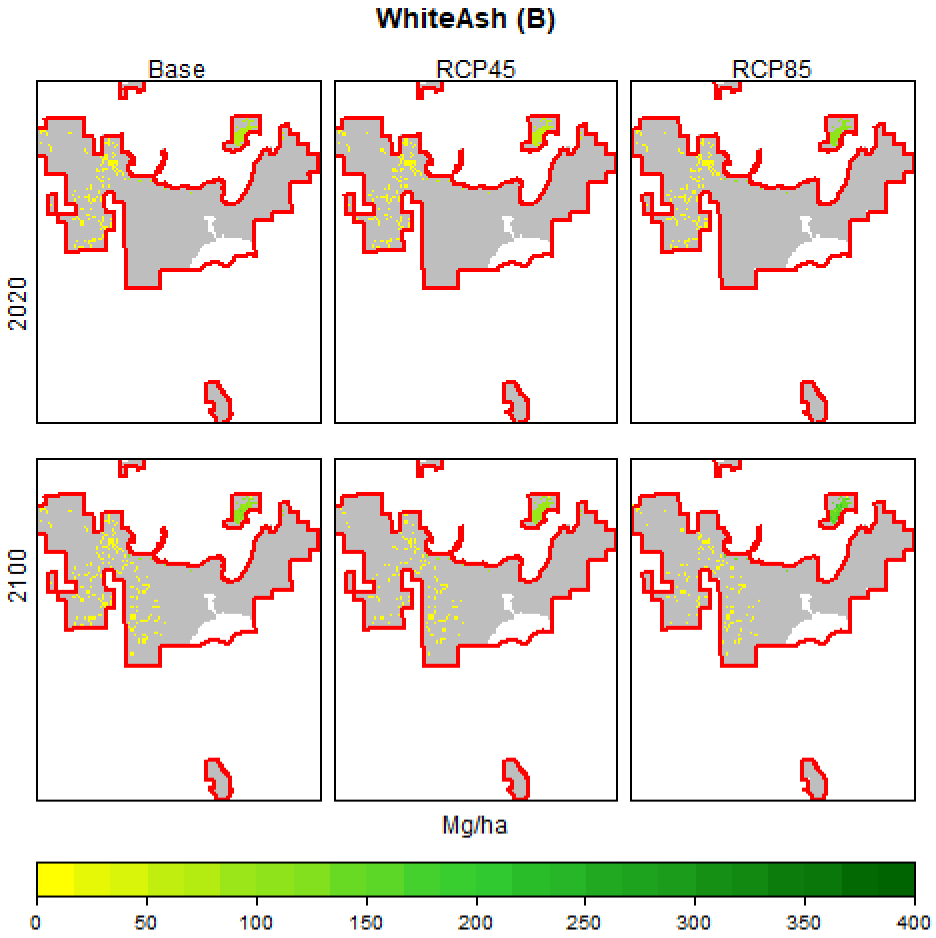

ShagbarkHickory (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

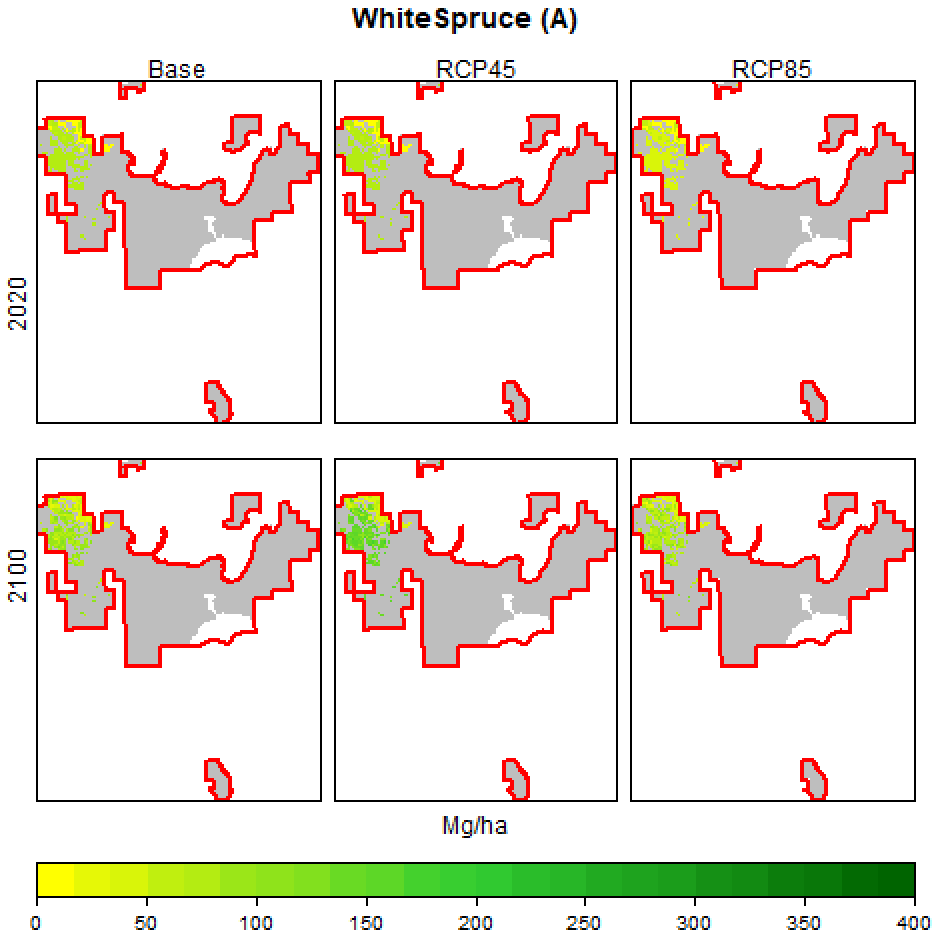

ShagbarkHickory (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

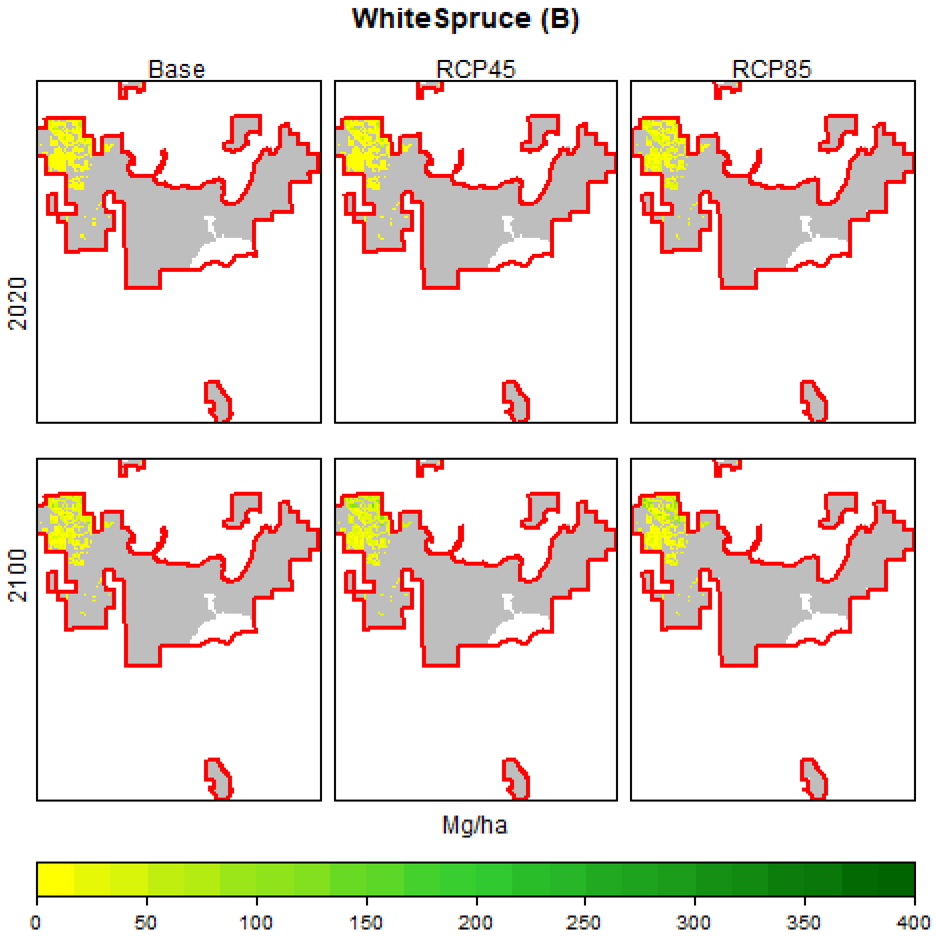

AmericanBeech (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

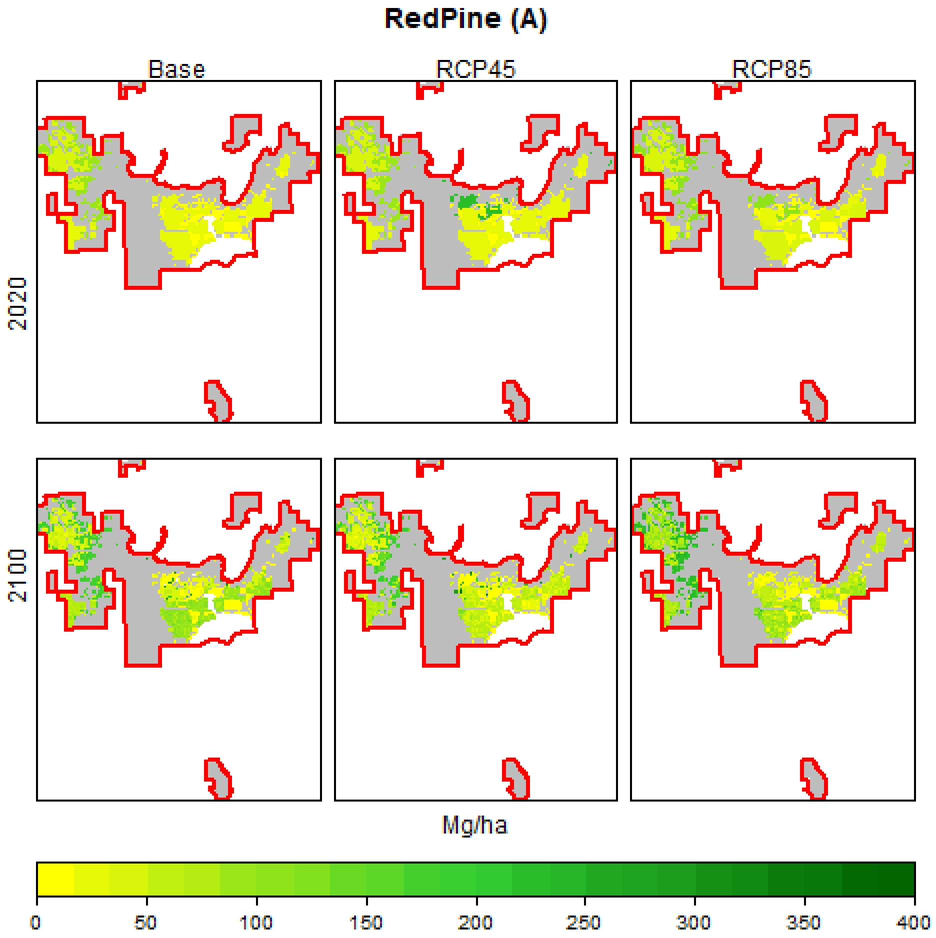

AmericanBeech (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

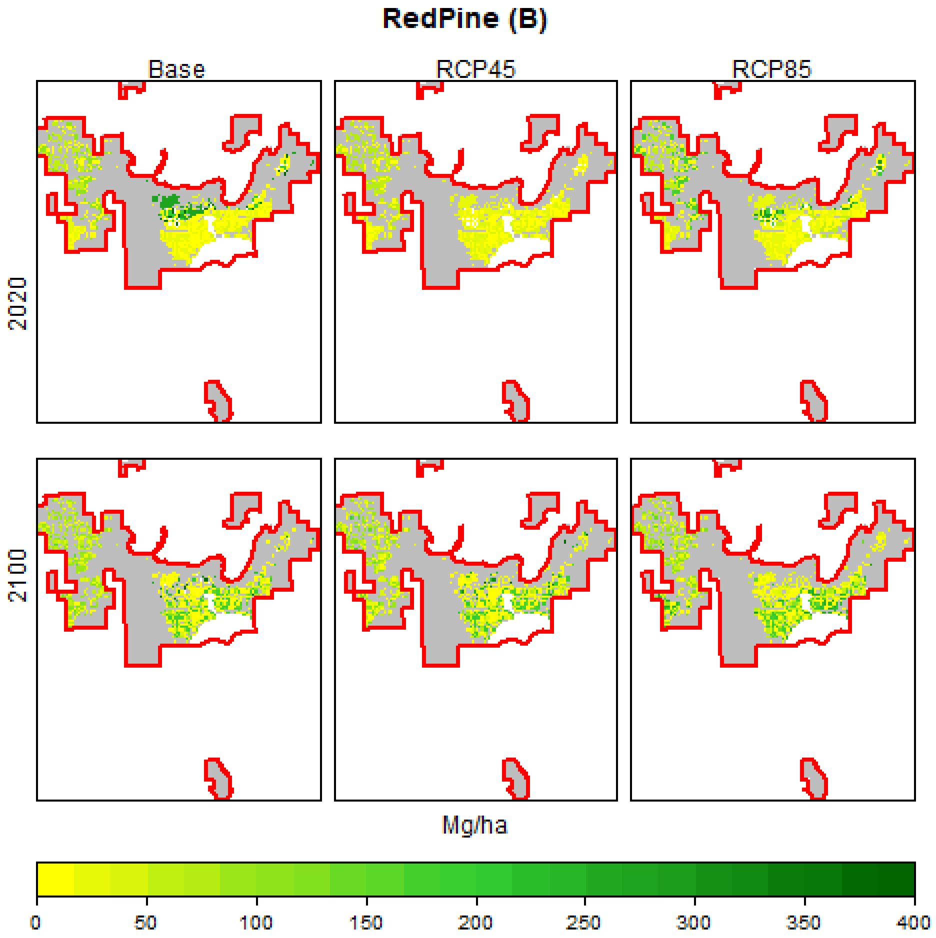

WhiteAsh (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

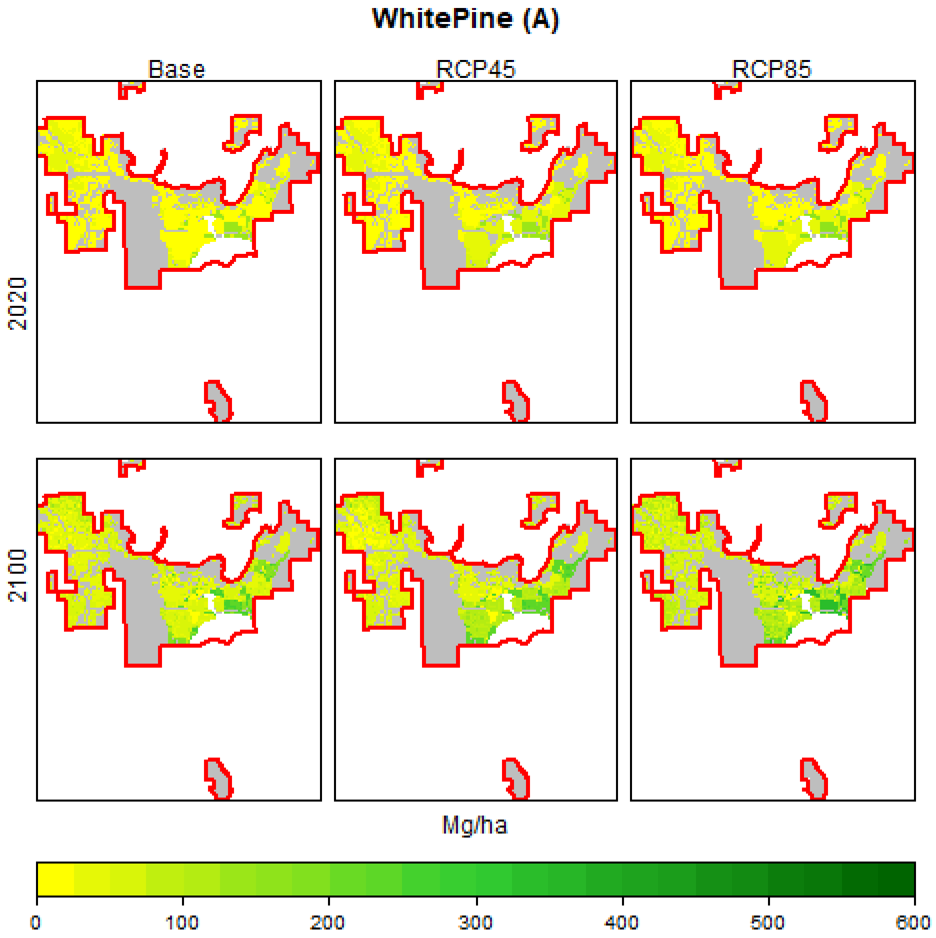

WhiteAsh (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

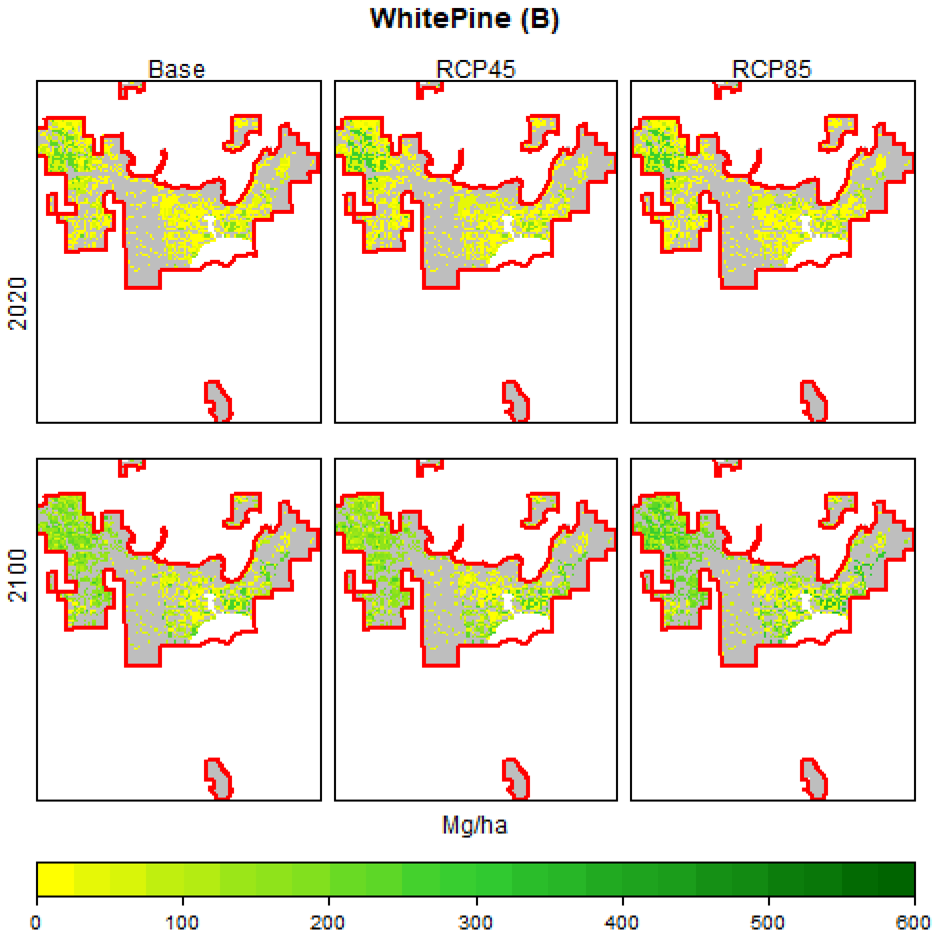

White Spruce (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

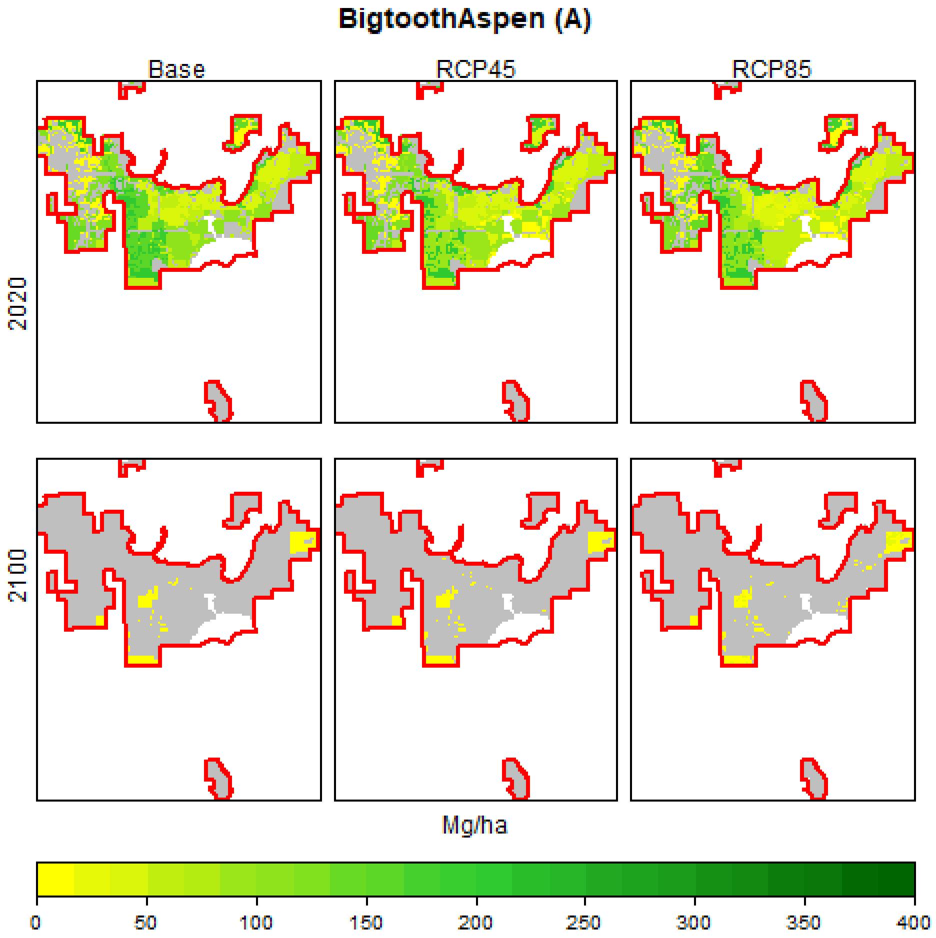

White Spruce (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

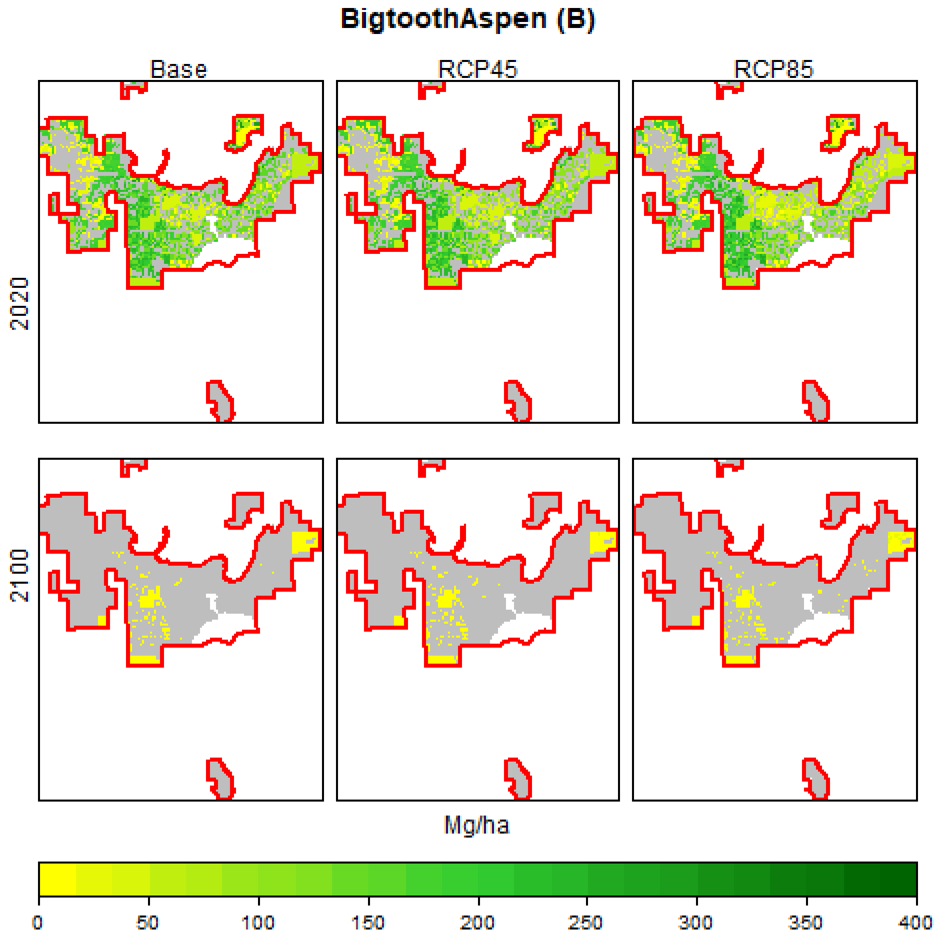

RedPine (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

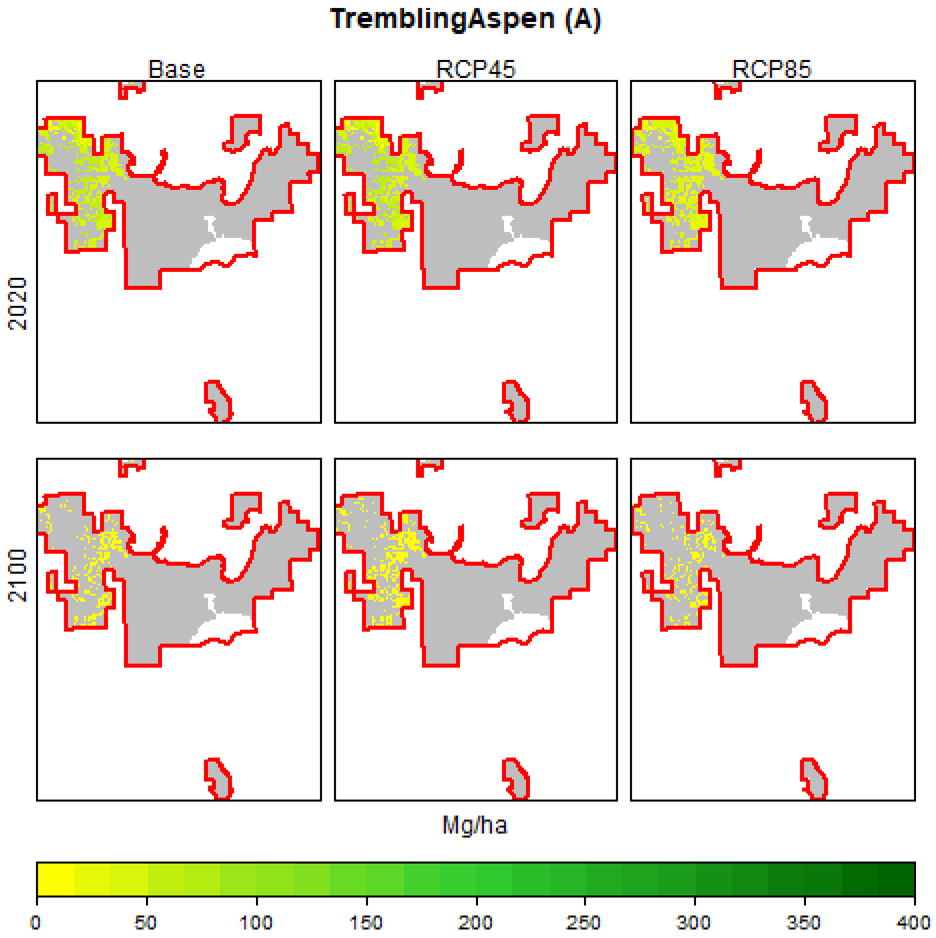

RedPine (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

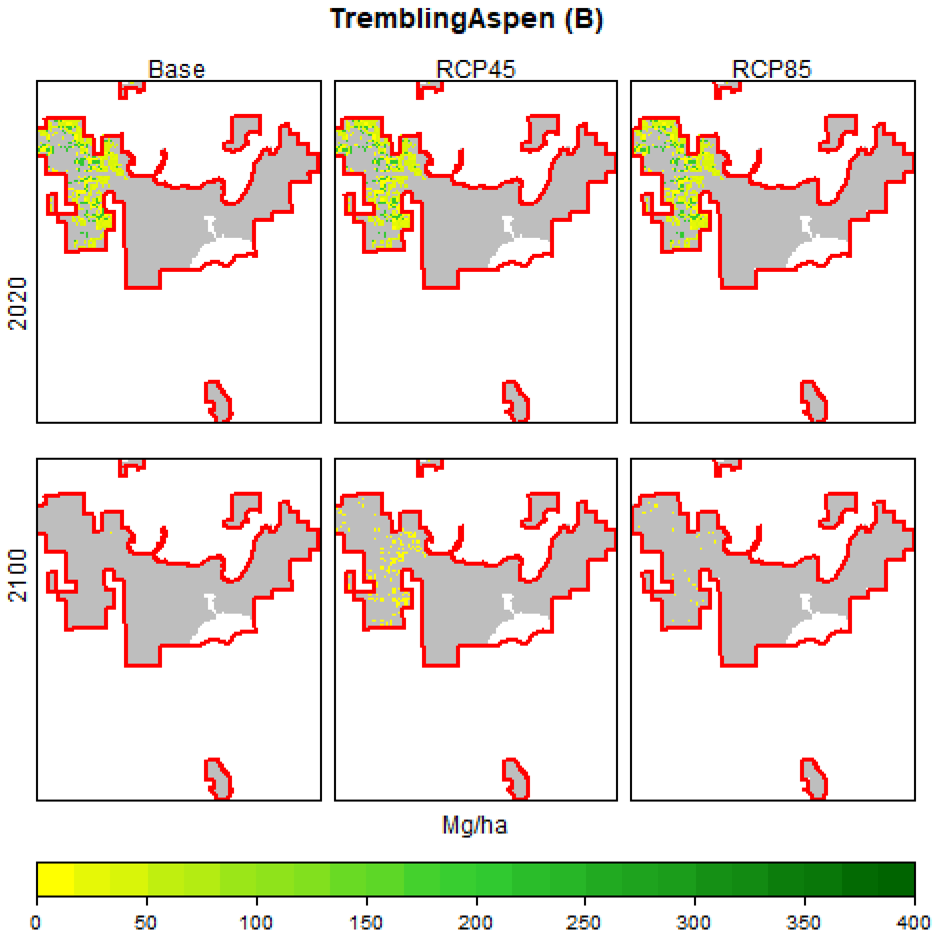

WhitePine (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
100
200
300
400
500
600

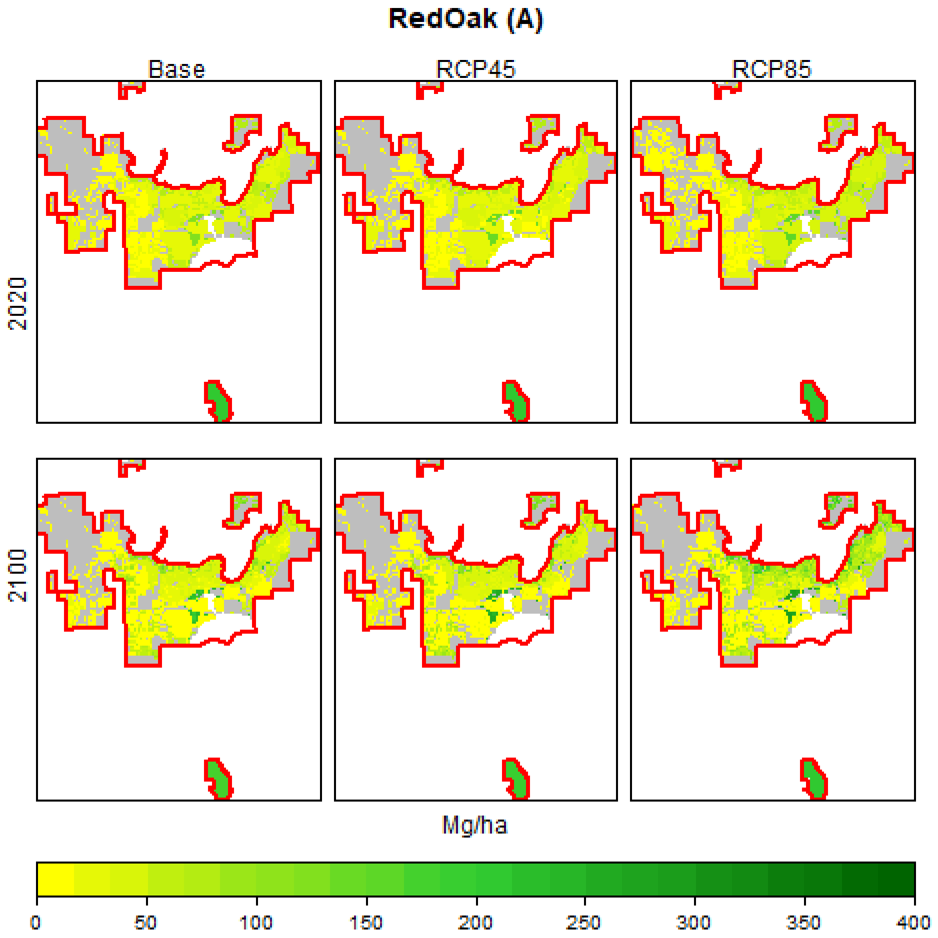

WhitePine (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
100
200
300
400
500
600

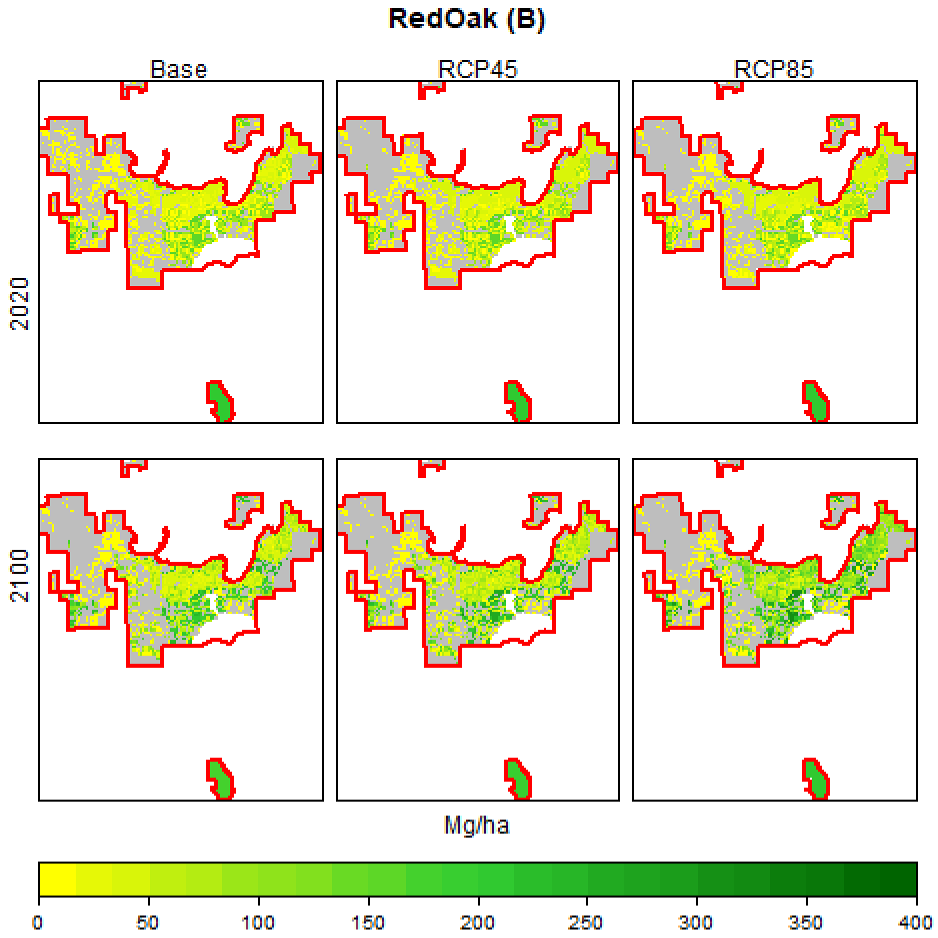

BigtoothAspen (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

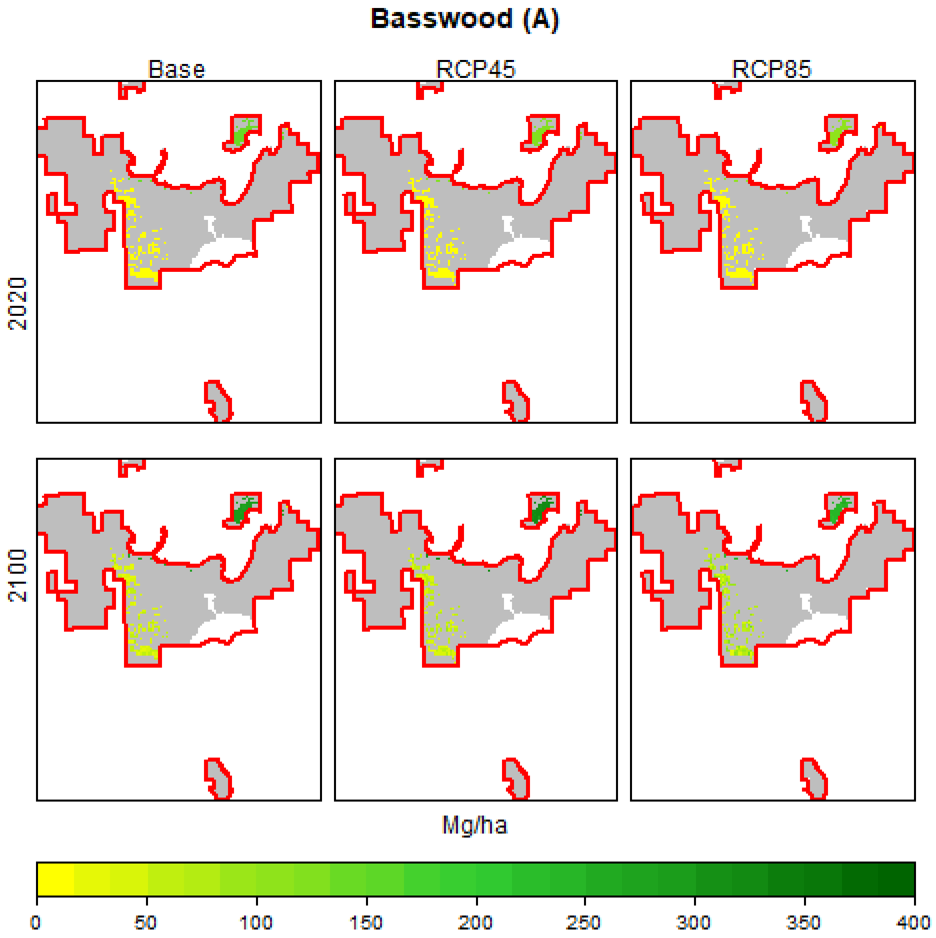

BigtoothAspen (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

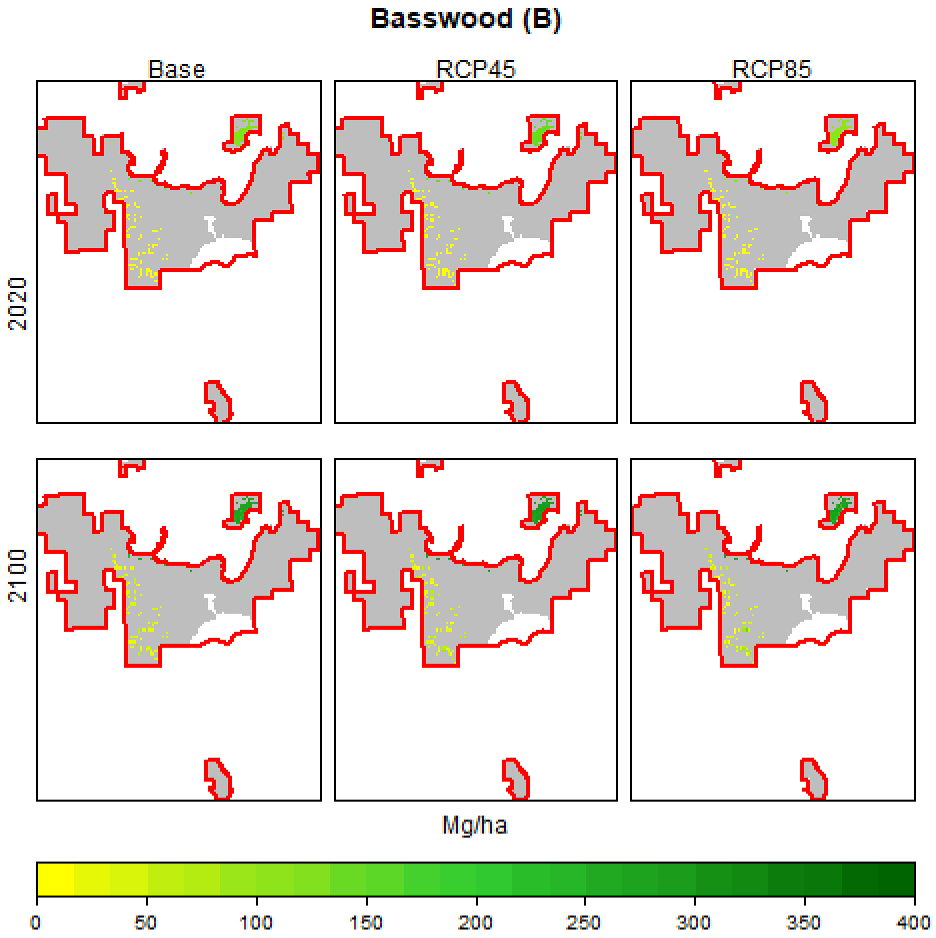

TremblingAspen (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

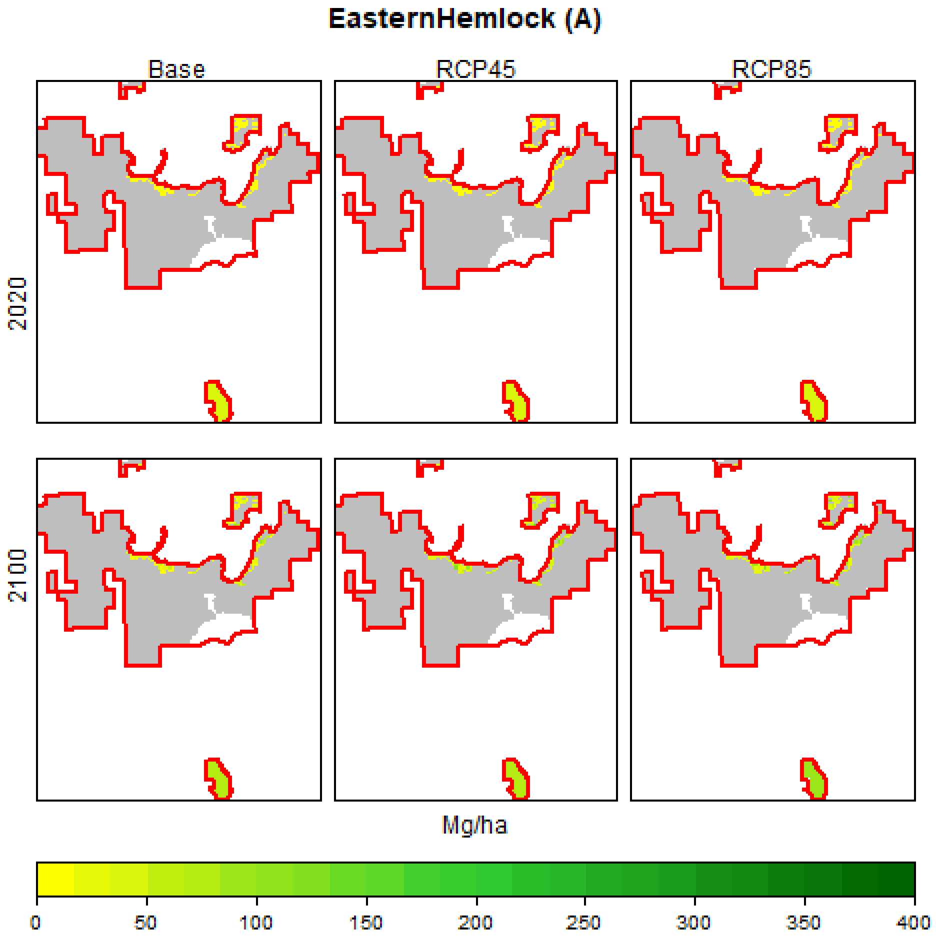

TremblingAspen (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

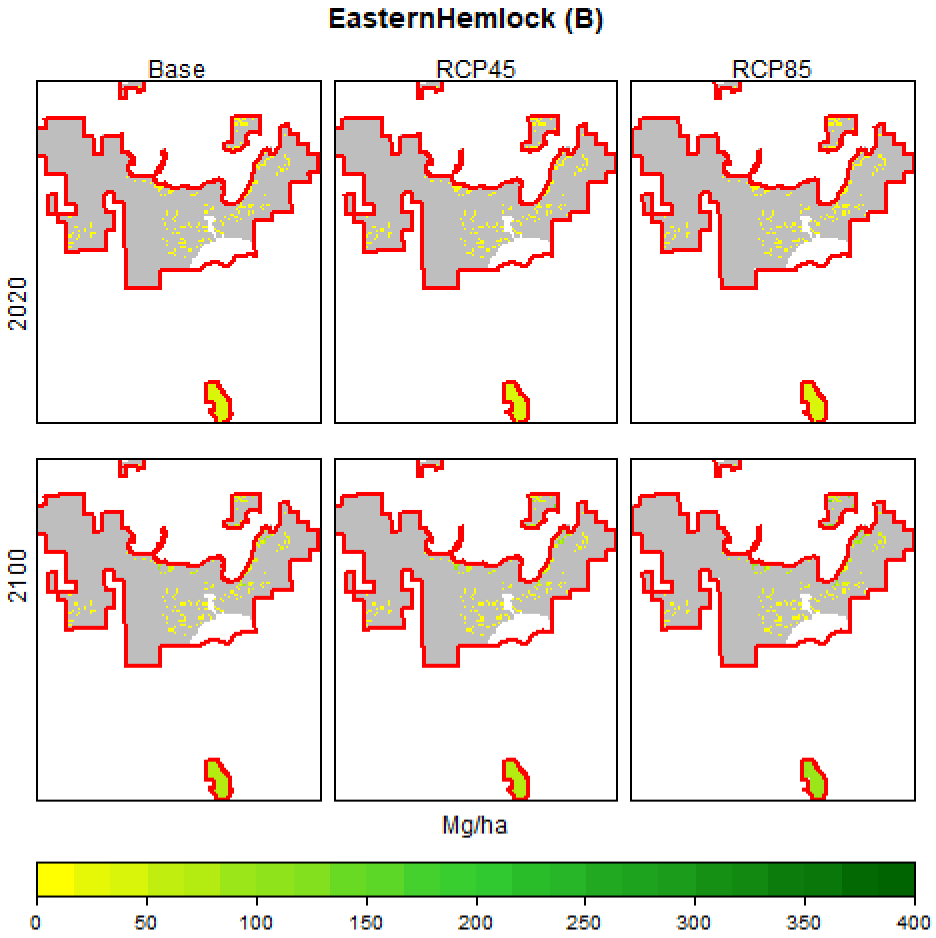

RedOak (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400


RedOak (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

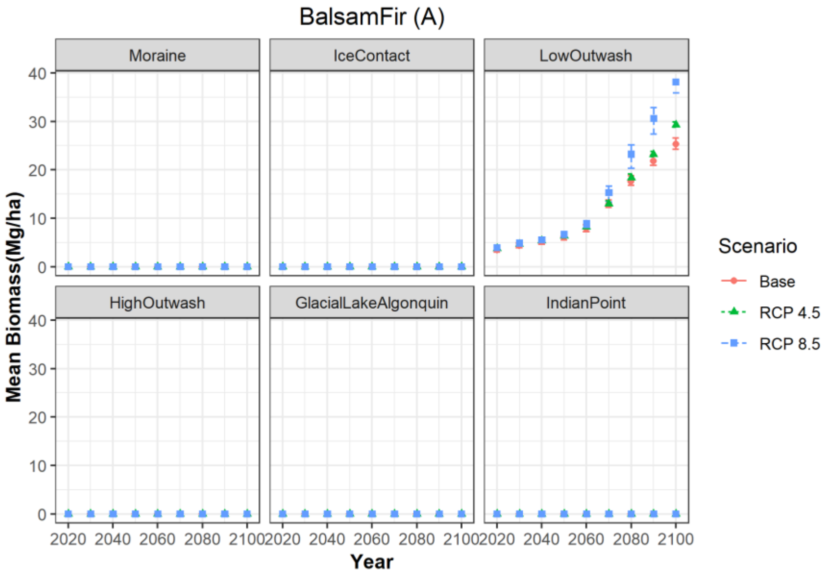

Basswood (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

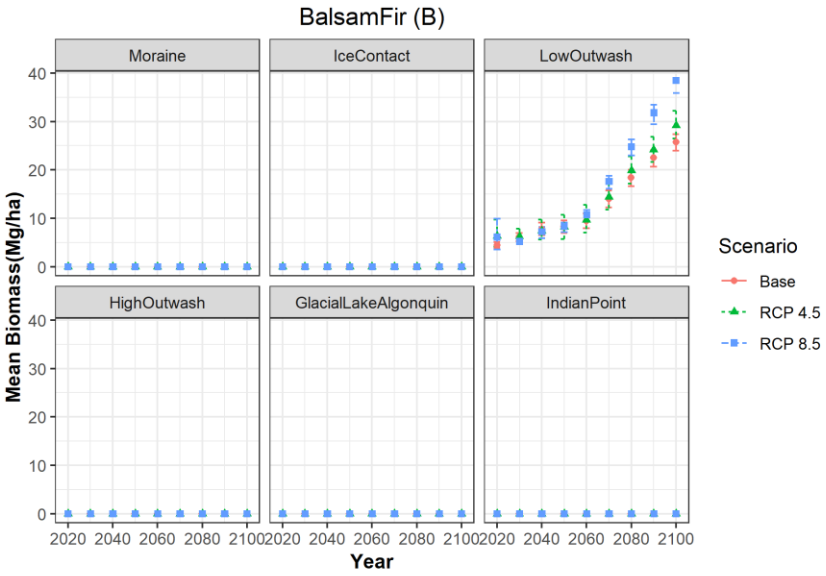

Basswood (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

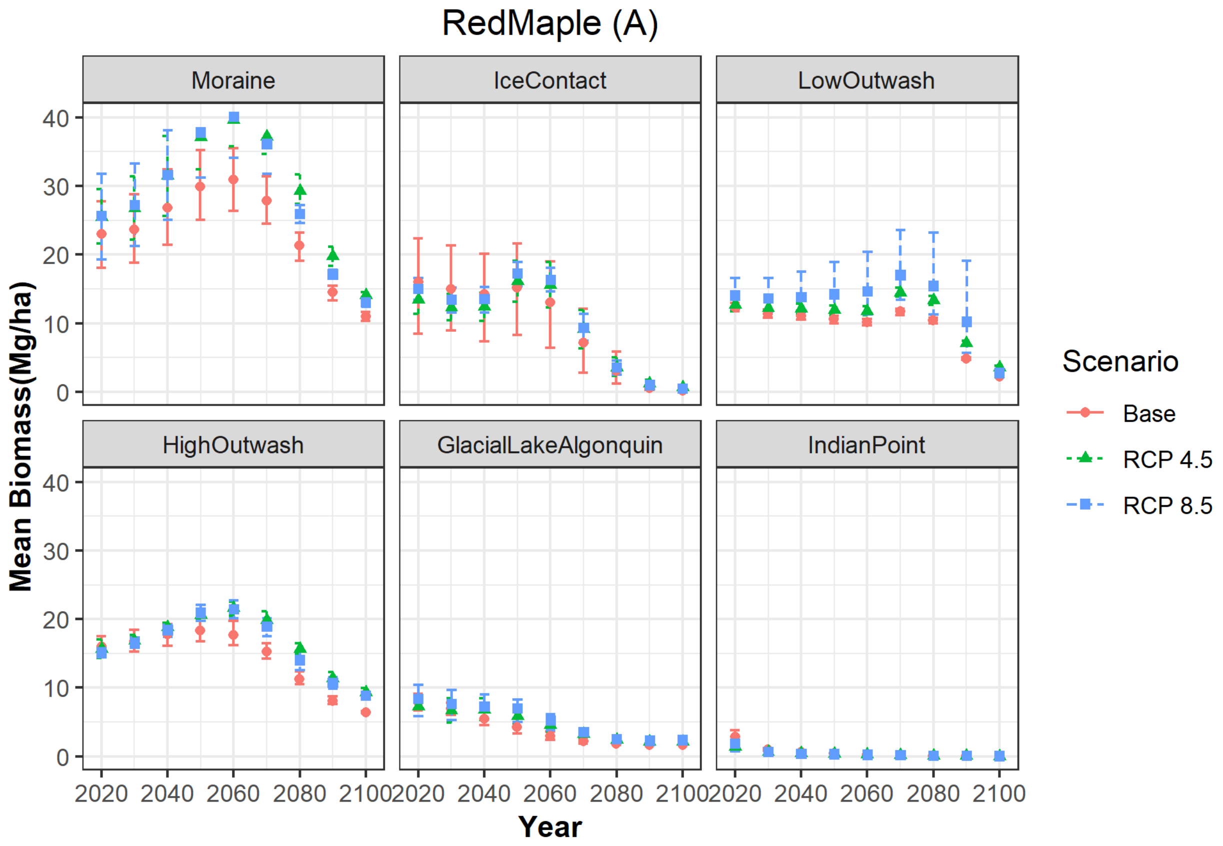

EasternHemlock (A)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

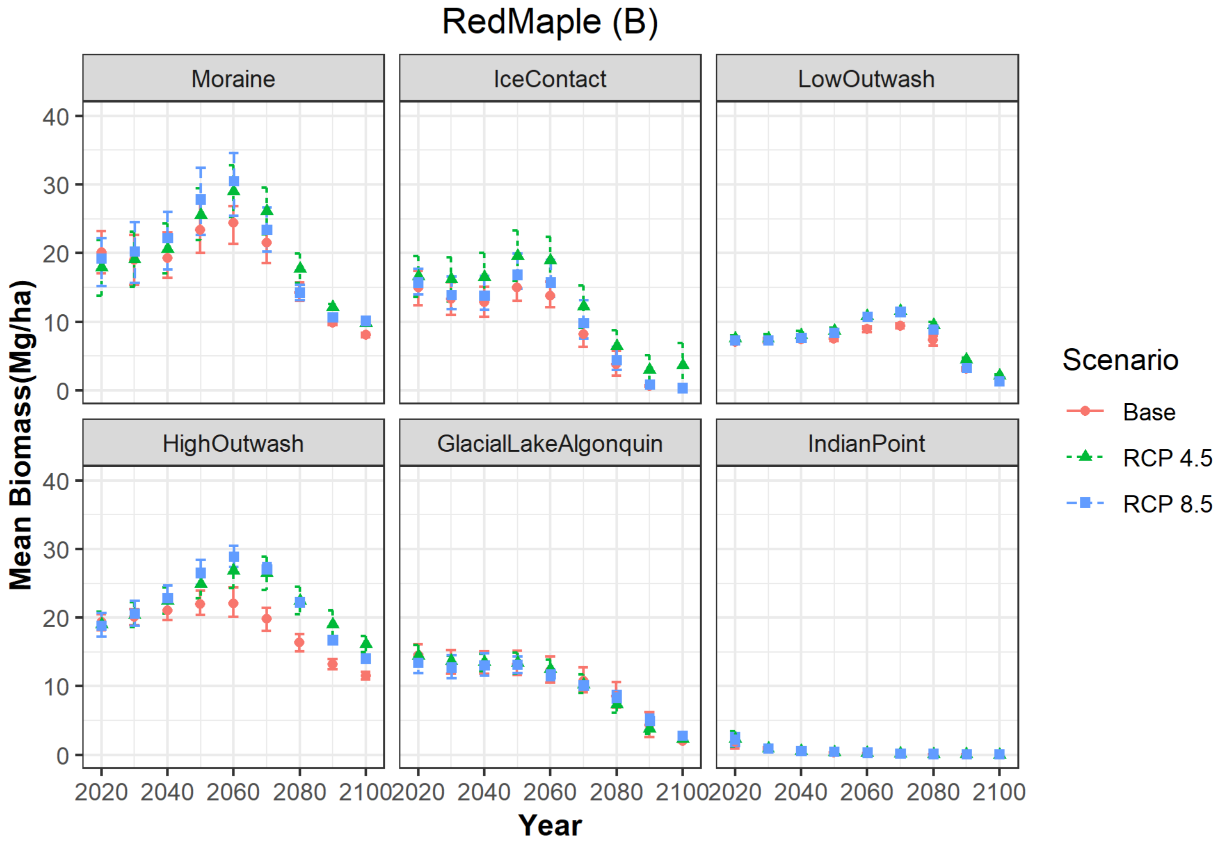

EasternHemlock (B)
Base
RCP45
RCP85
2020
2100
Mg/ha
0
50
100
150
200
250
300
350
400

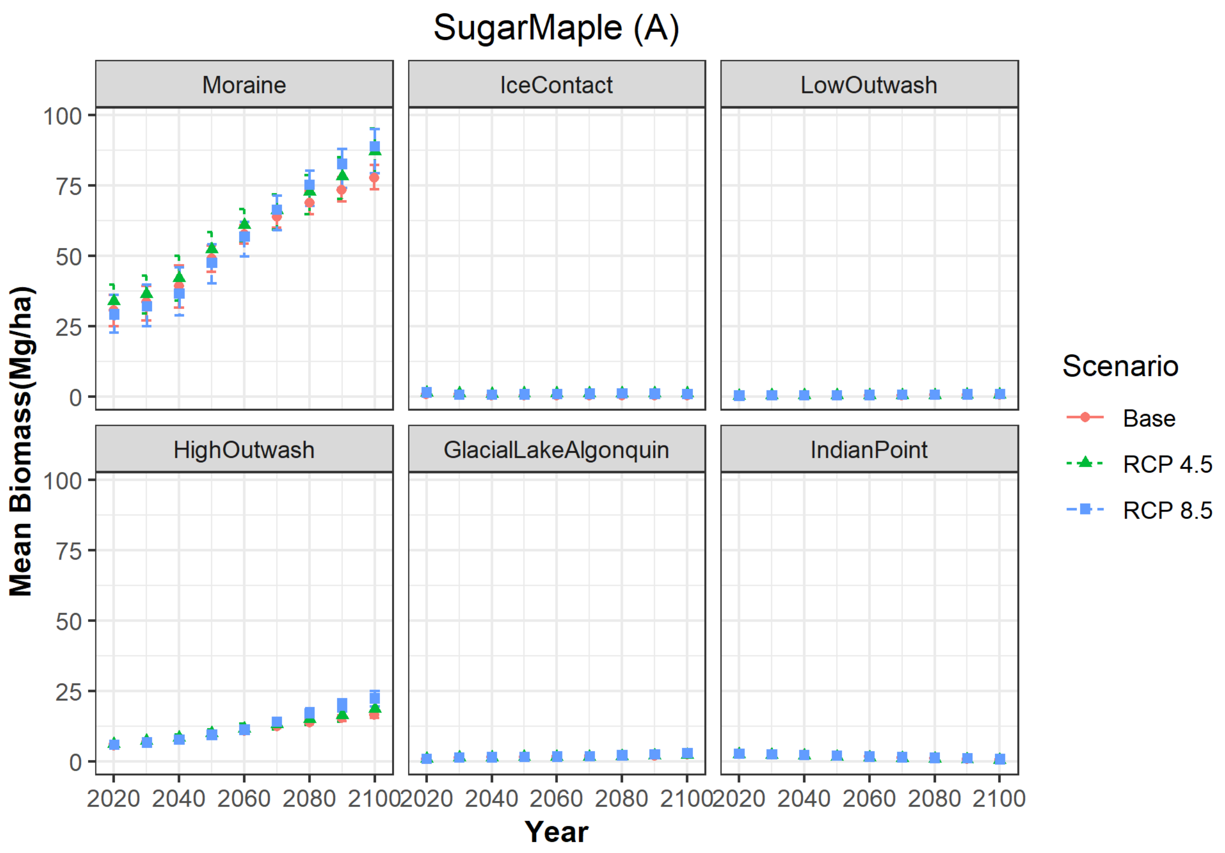
APPENDIX FIGURE G: Given are figures displaying the mean and standard deviation across time for three climate scenarios. Each species has two figures. The first figure, labeled A, displays the results given by using the first input map. The second, labelled B, displays the results given by the second randomly generated input map. The species are listed in alphabetical order for their scientific name. The figures given for shagbark hickory come from a separate set of model runs that included it as a species, unlike the other figures.

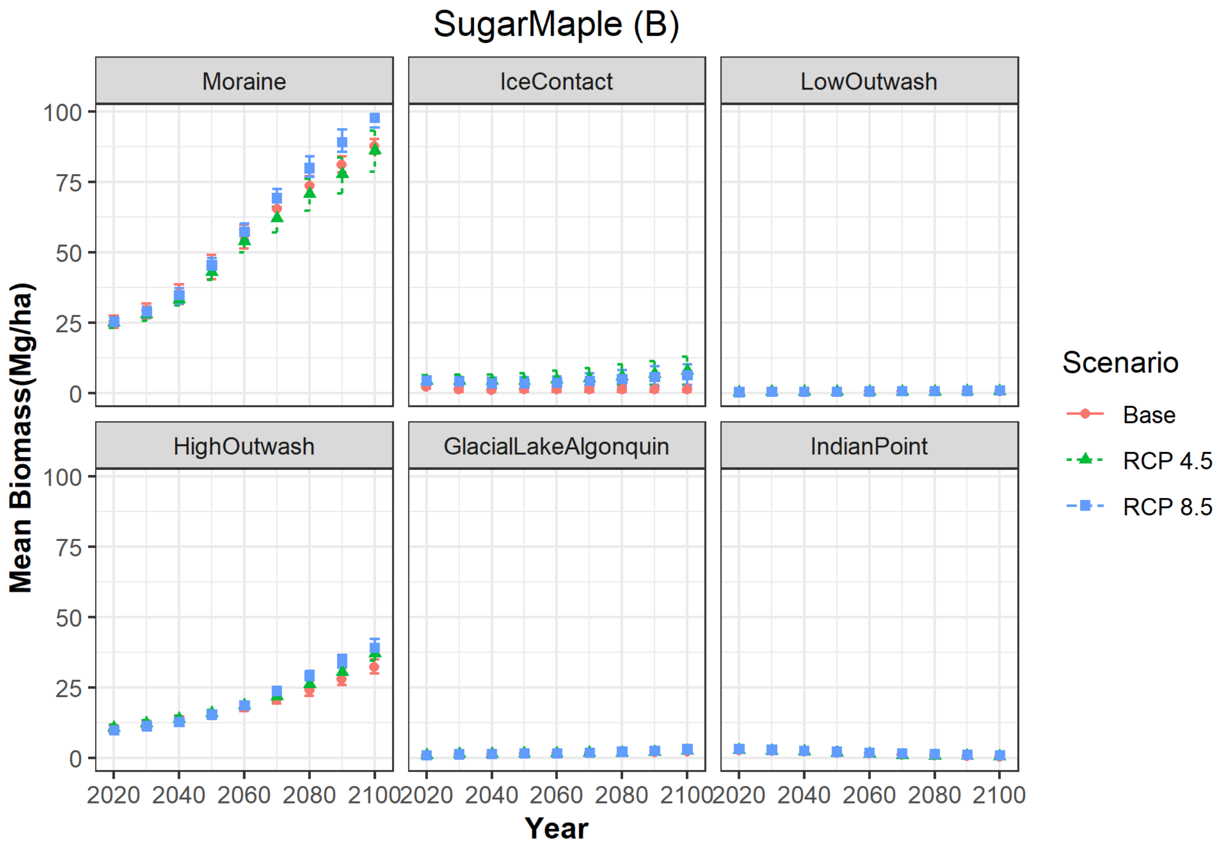


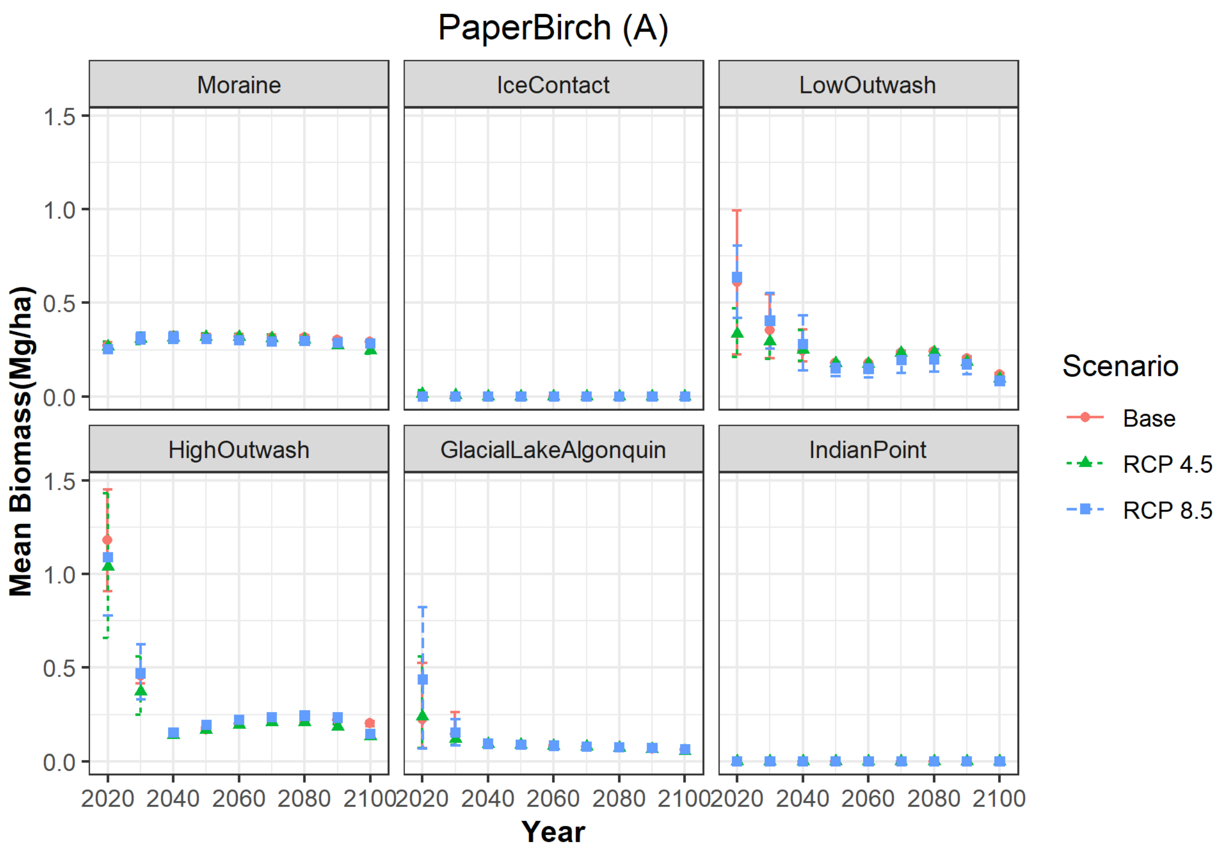



RedMaple (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
0
10
20
30
40
2020
2040
2060
2080
2100
Year
Scenario
Base
RCP 4.5
RCP 8.5


RedMaple (B)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
0
10
20
30
40
2020
2040
2060
2080
2100
Year
Scenario
Base
RCP 4.5
RCP 8.5


SugarMaple (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
100
75
50
25
0
2020
2040
2060
2080
2100
Year
Scenario
Base
RCP 4.5
RCP 8.5


SugarMaple (B)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
100
75
50
25
0
2020
2040
2060
2080
2100
Year
Scenario
Base
RCP 4.5
RCP 8.5


PaperBirch (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
0.0
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Year
Scenario
Base
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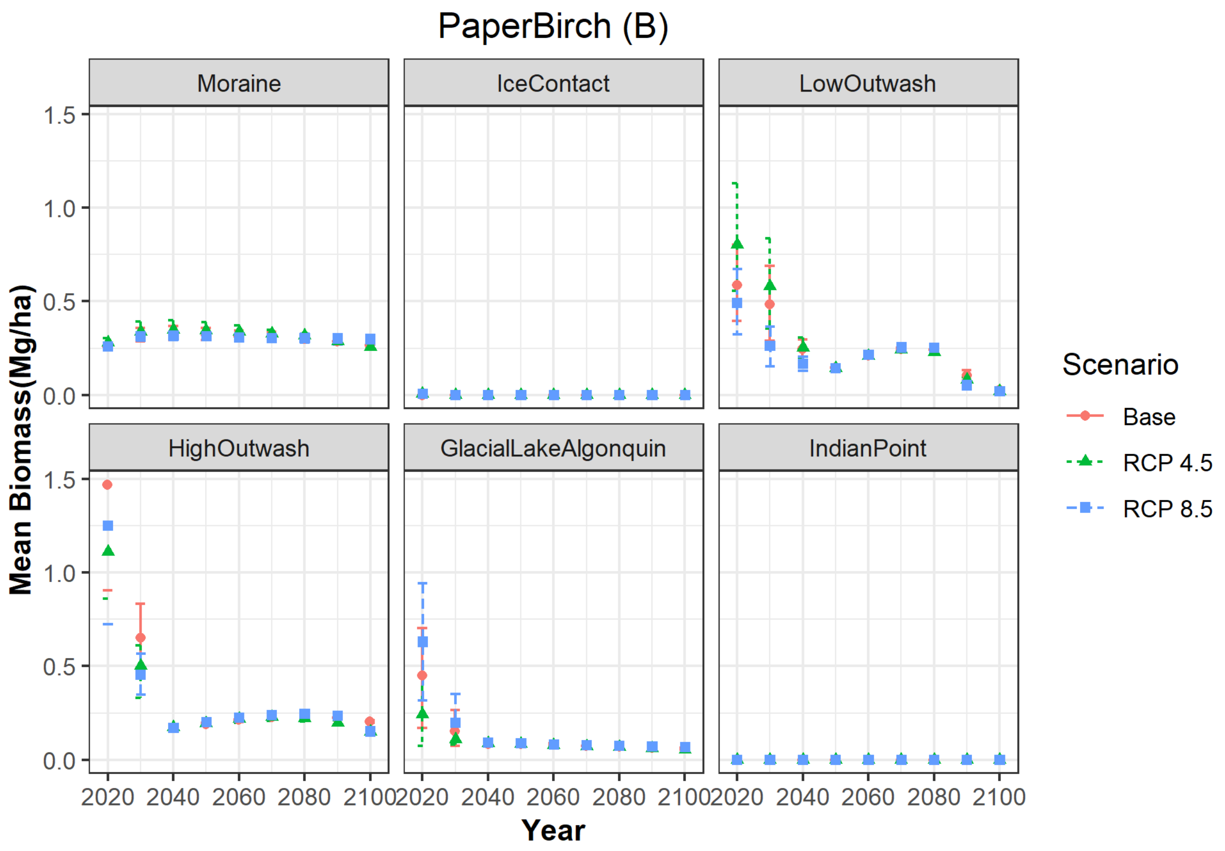
RCP 8.5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Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Year
Scenario
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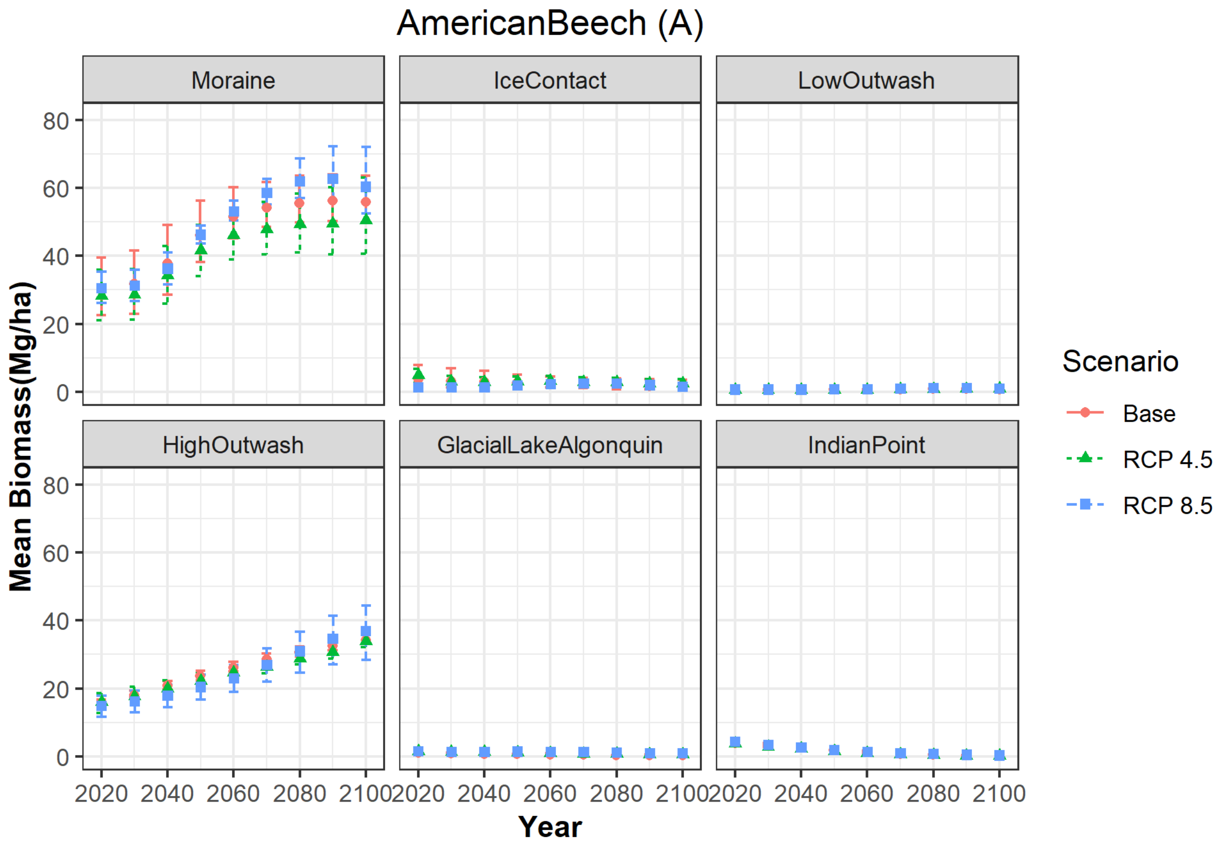
RCP 8.5


AmericanBeech (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Year
Scenario
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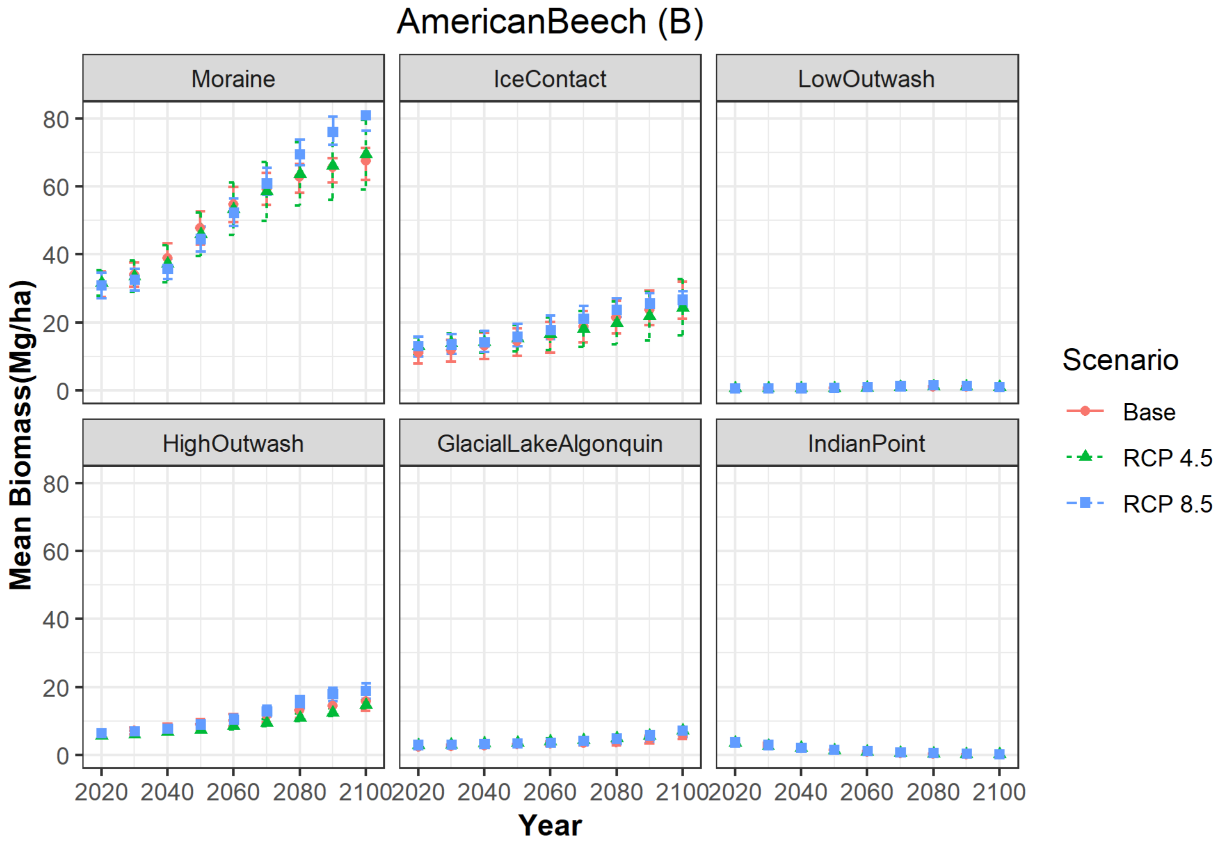
AmericanBeech (B)
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GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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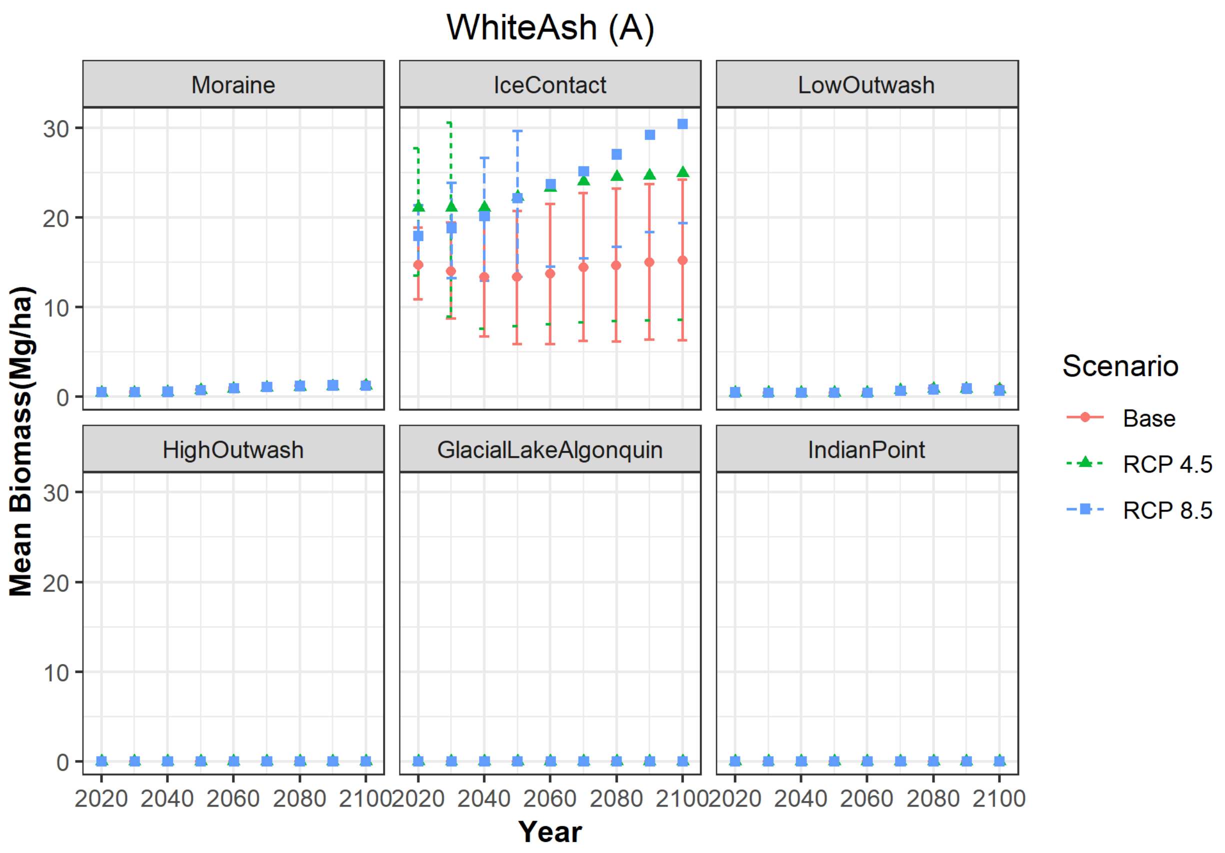
RCP 8.5


WhiteAsh (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Year
Scenario
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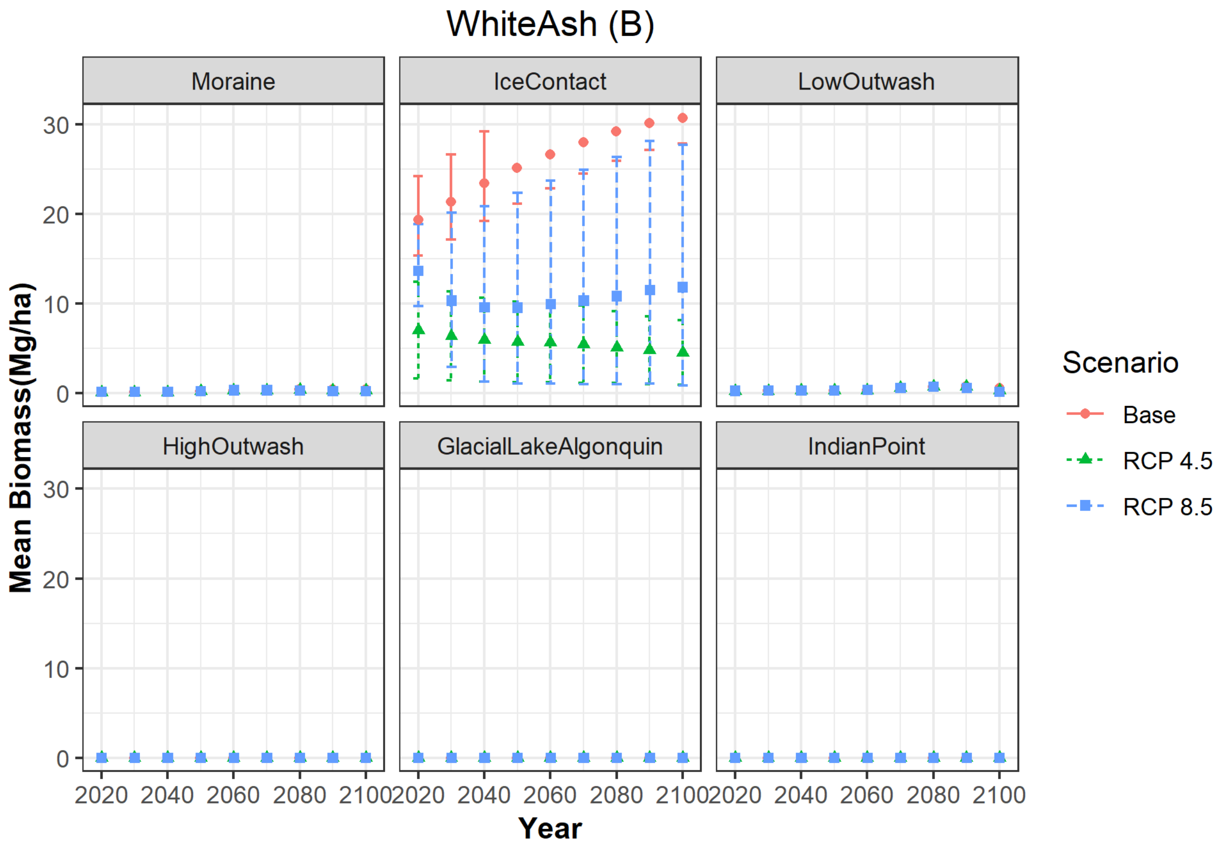
RCP 4.5
RCP 8.5


WhiteAsh (B)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Scenario
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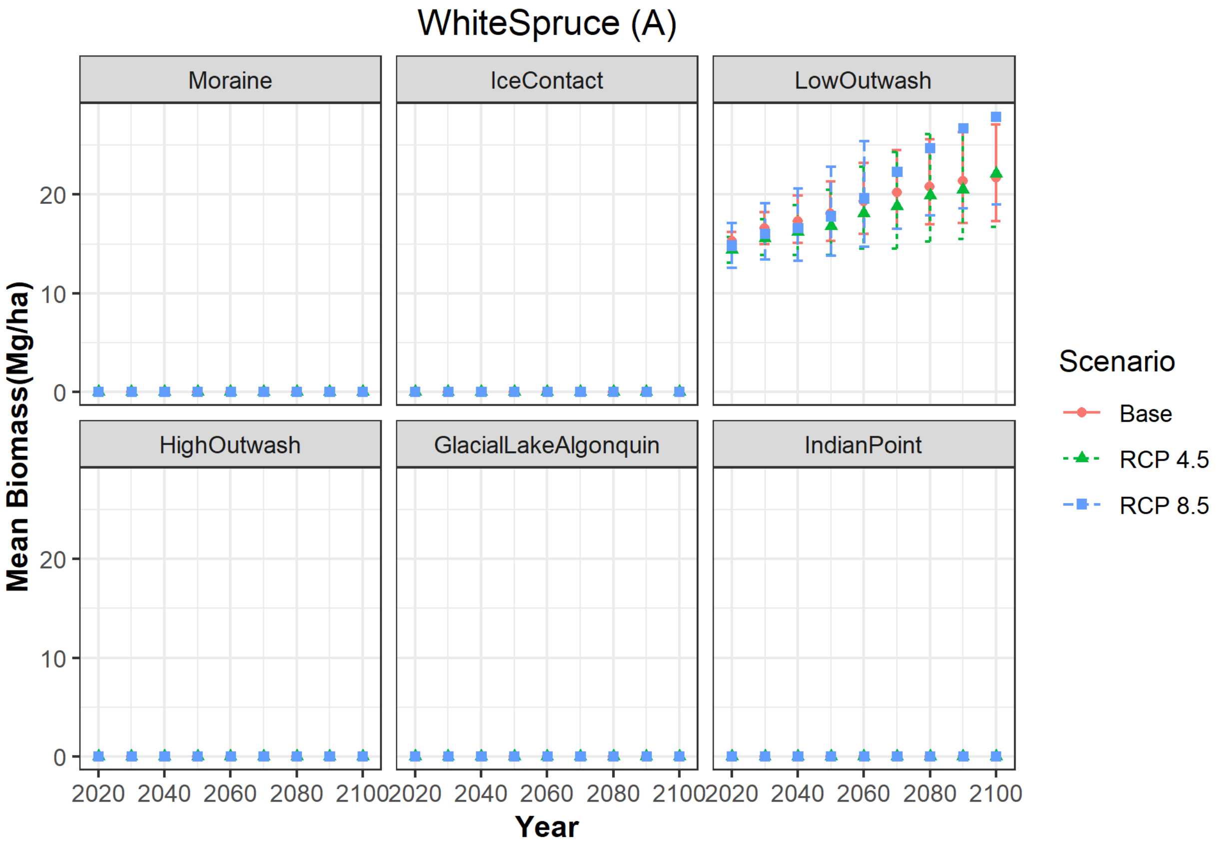
RCP 8.5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Moraine
IceContact
LowOutwash
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IndianPoint
Mean Biomass(Mg/ha)
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Scenario
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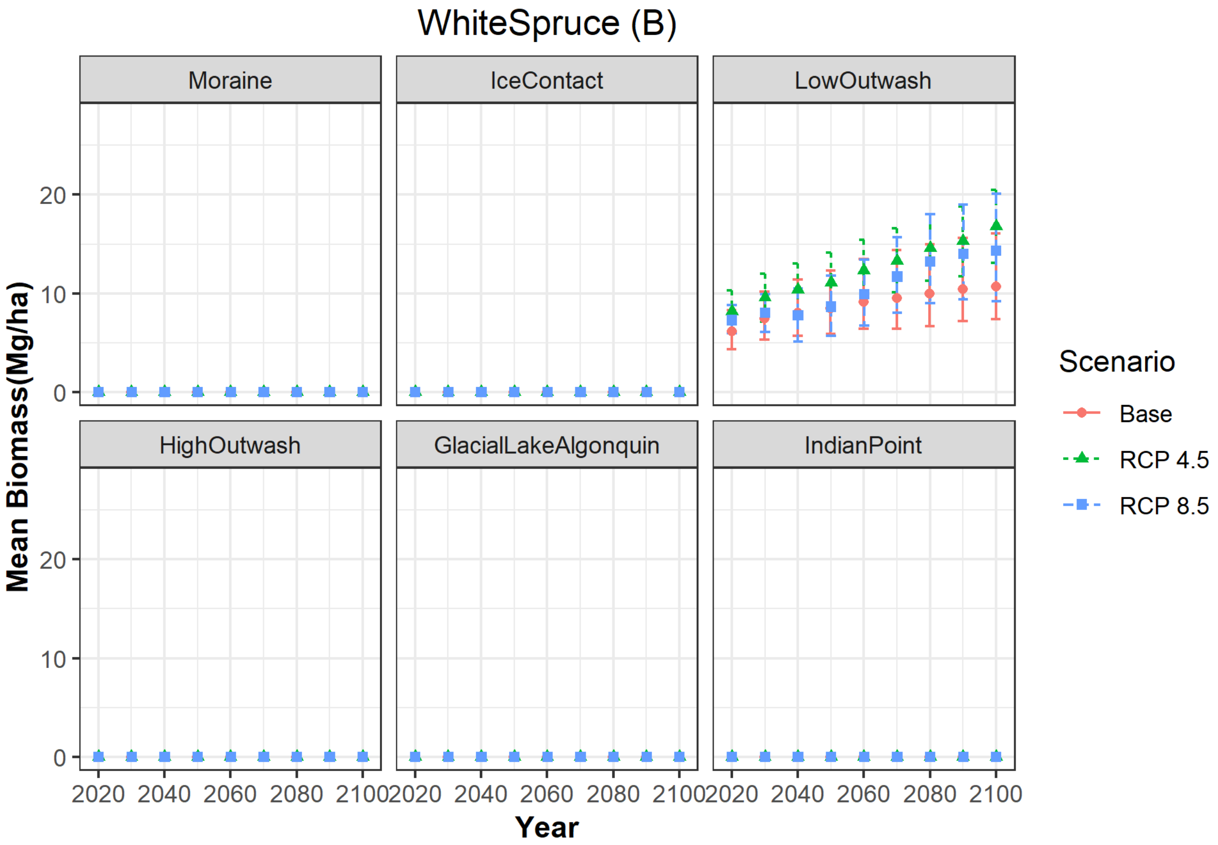
RCP 8.5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Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Year
Scenario
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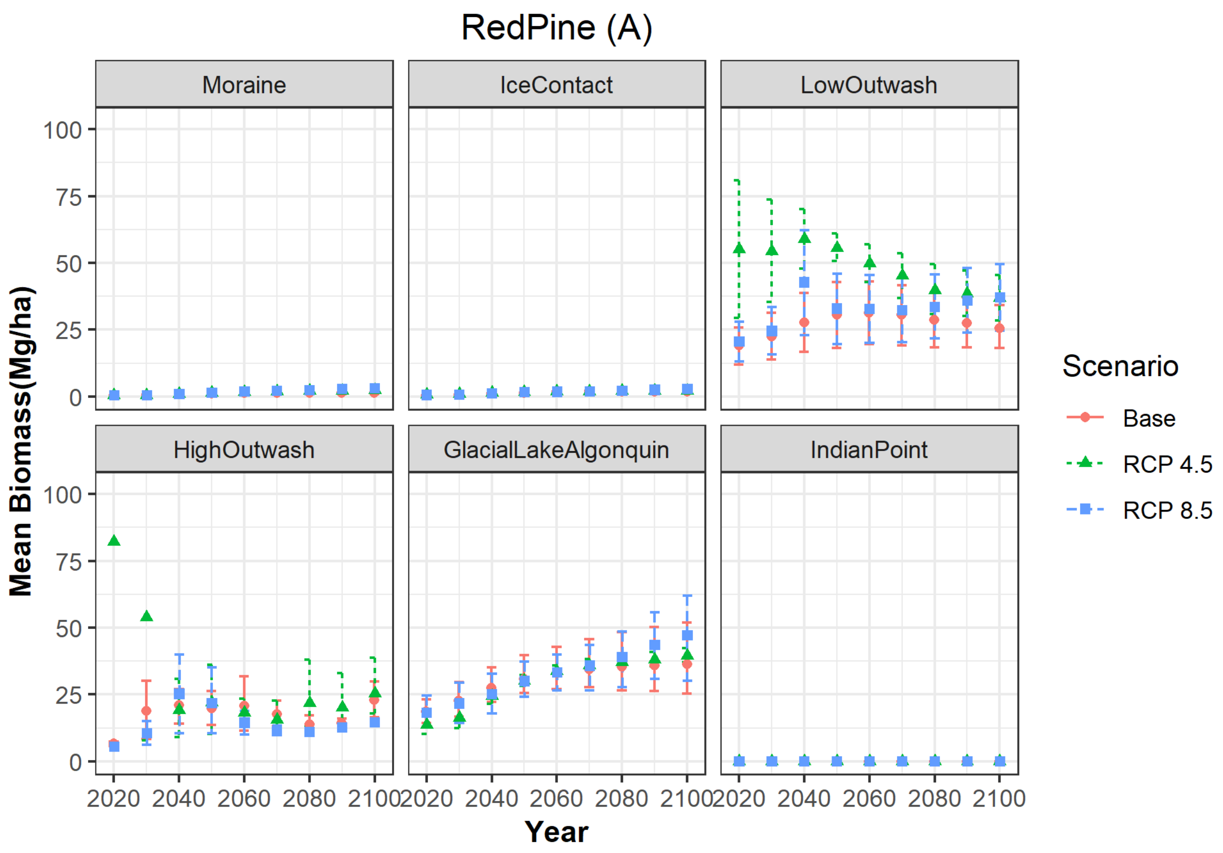
RCP 8.5


RedPine (A)
Moraine
IceContact
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HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Year
Scenario
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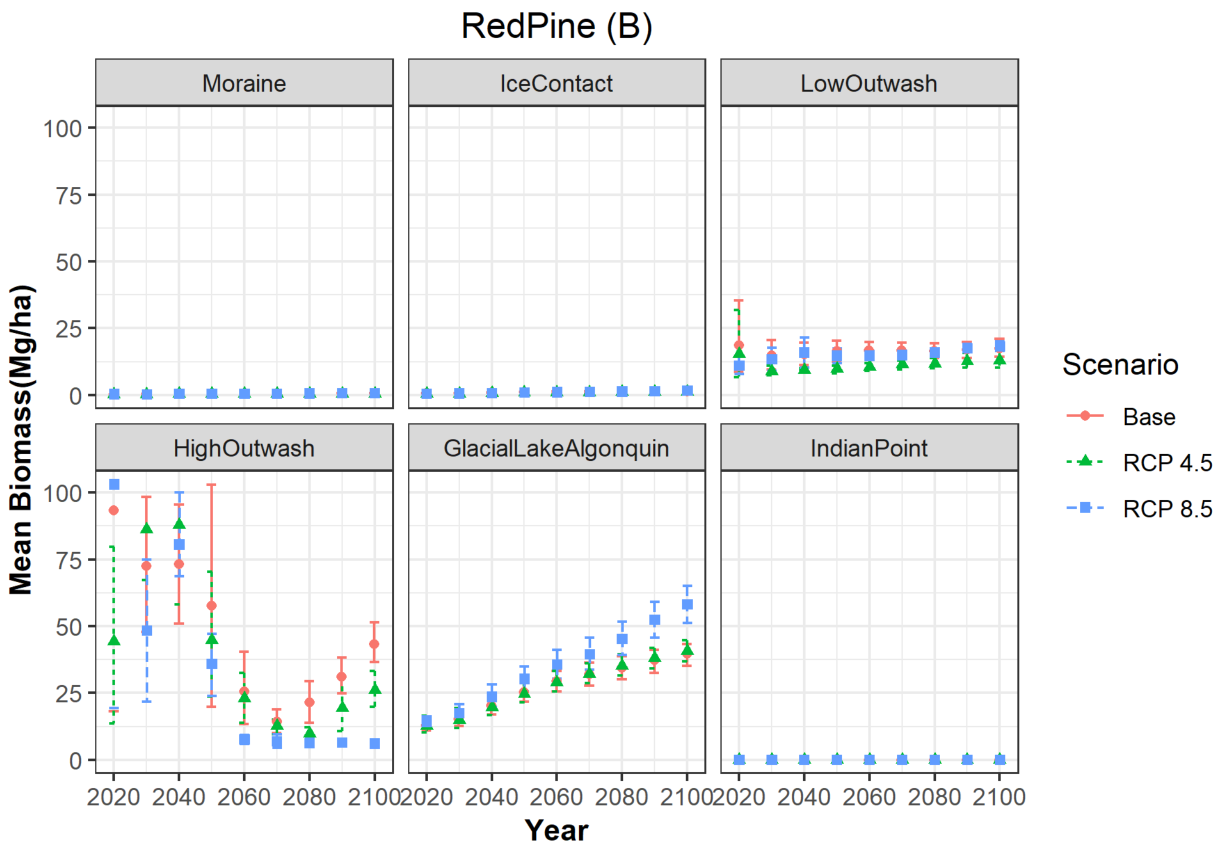
RCP 4.5
RCP 8.5


RedPine (B)
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HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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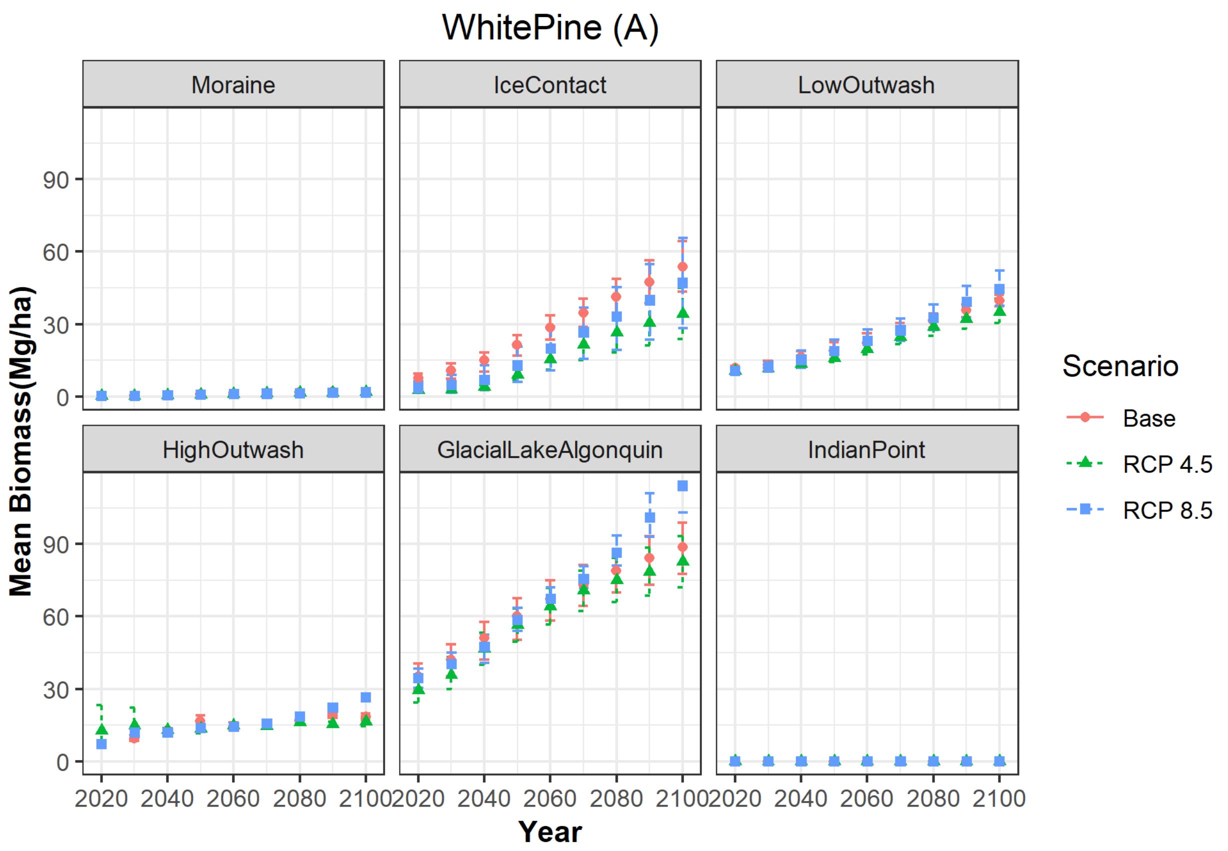
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IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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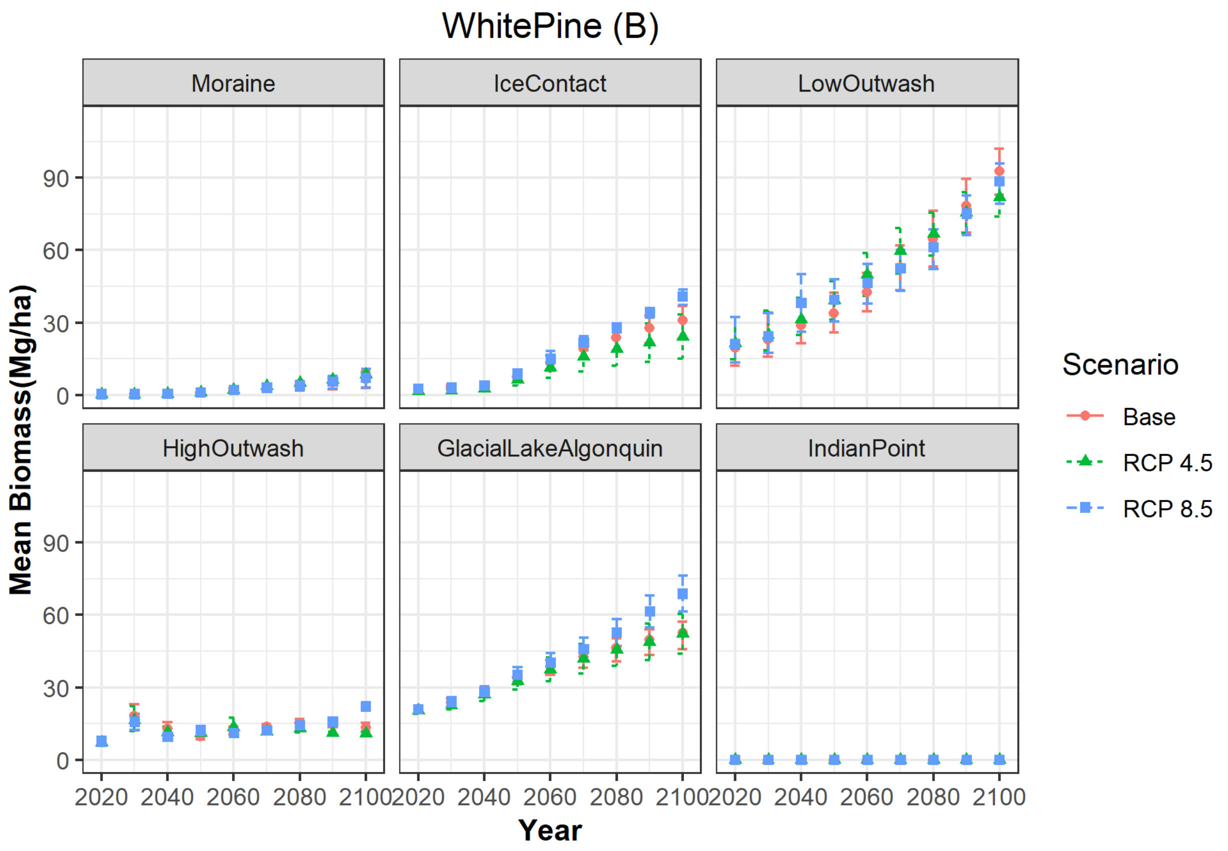
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GlacialLakeAlgonquin
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Mean Biomass(Mg/ha)
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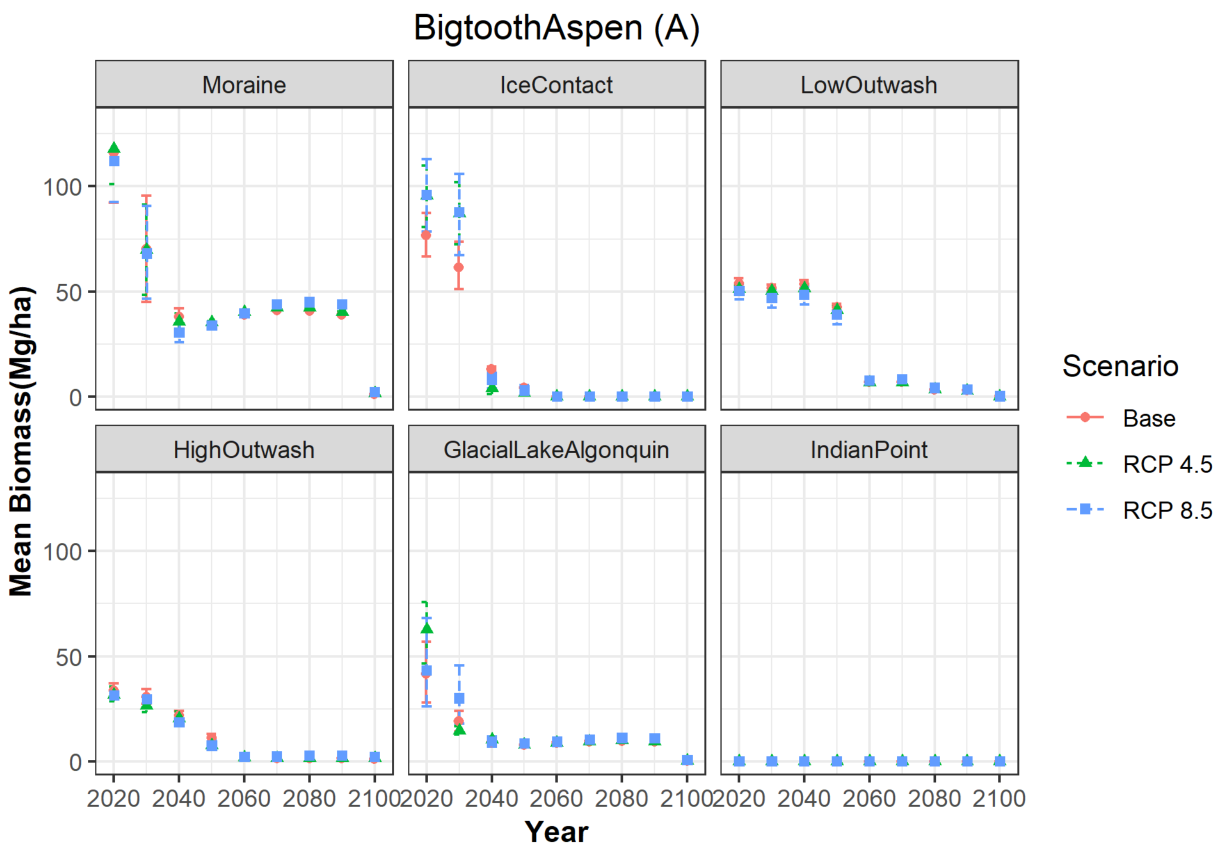
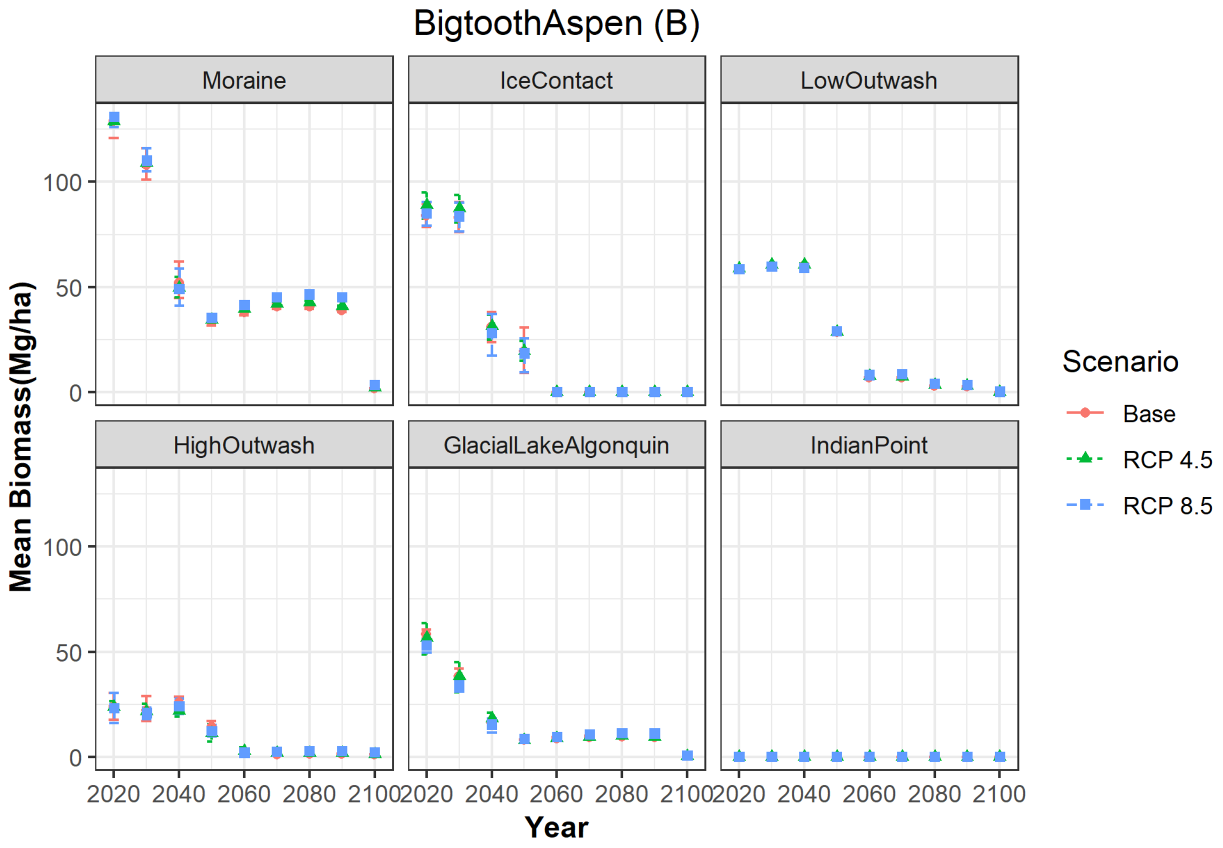

BigtoothAspen (A)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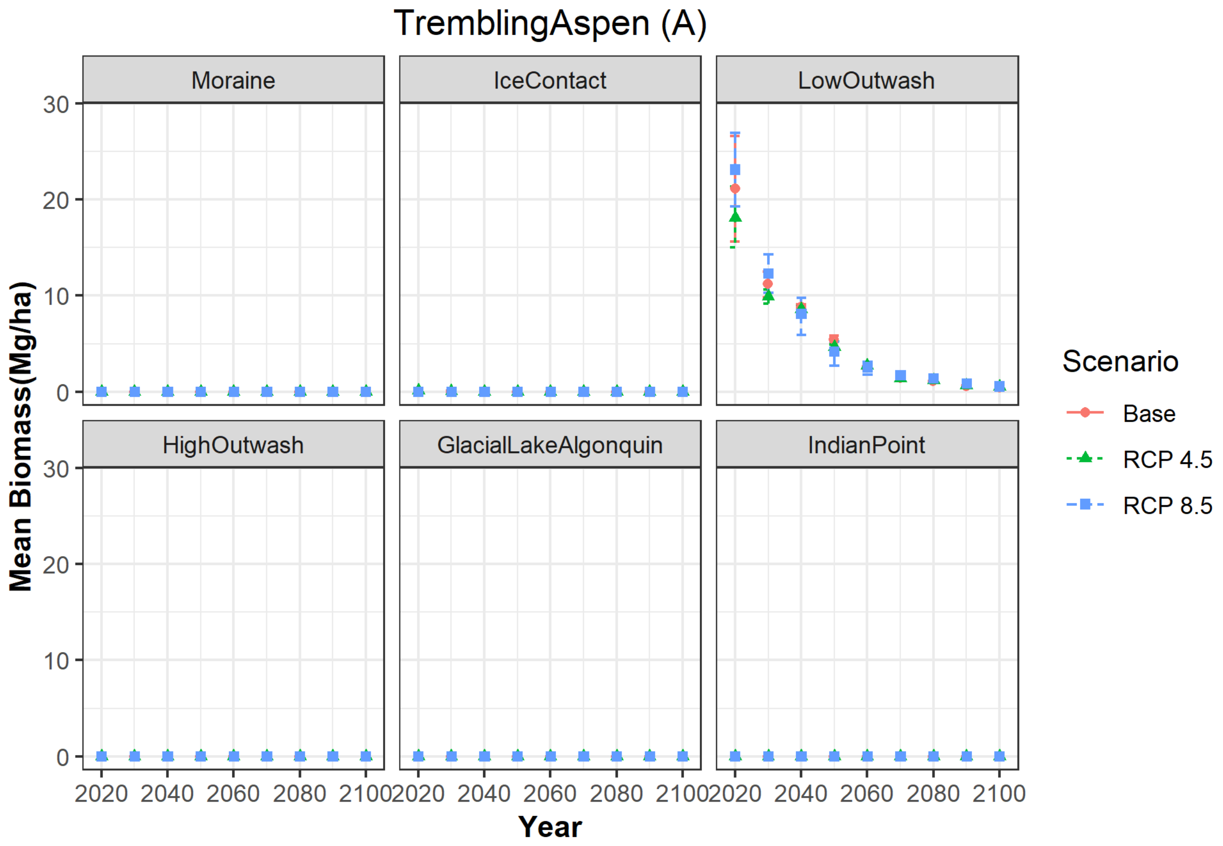
TremblingAspen (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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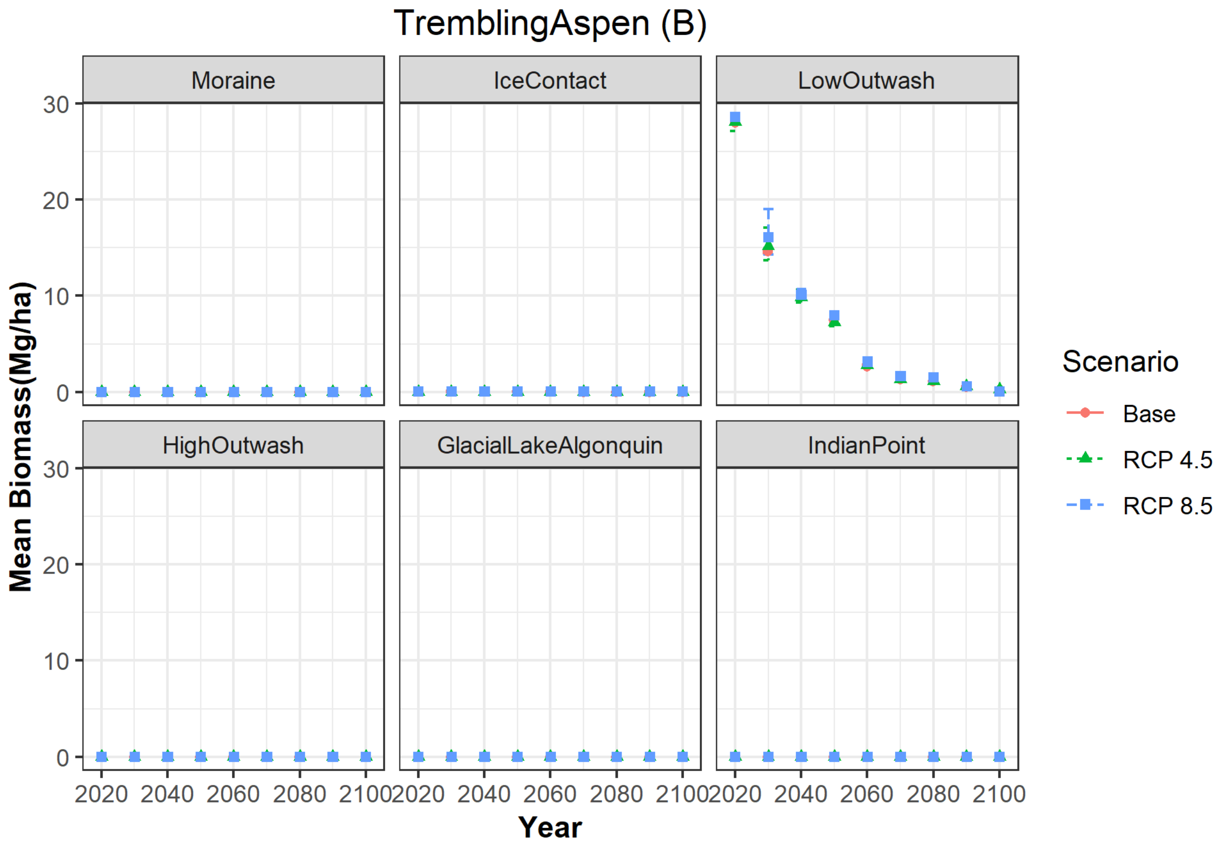
Year
Scenario
Base
RCP 4.5
RCP 8.5


TremblingAspen (B)
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HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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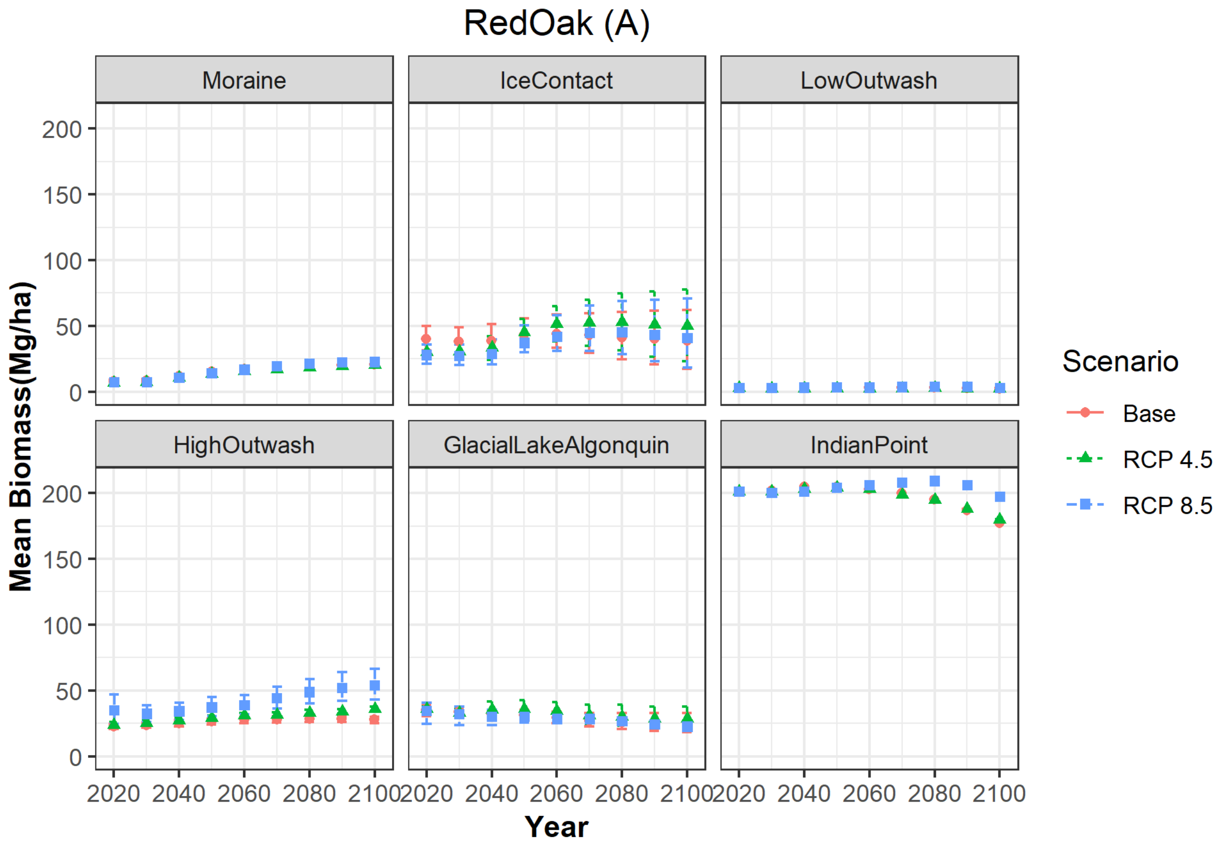
Scenario
Base
RCP 4.5
RCP 8.5


RedOak (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Scenario
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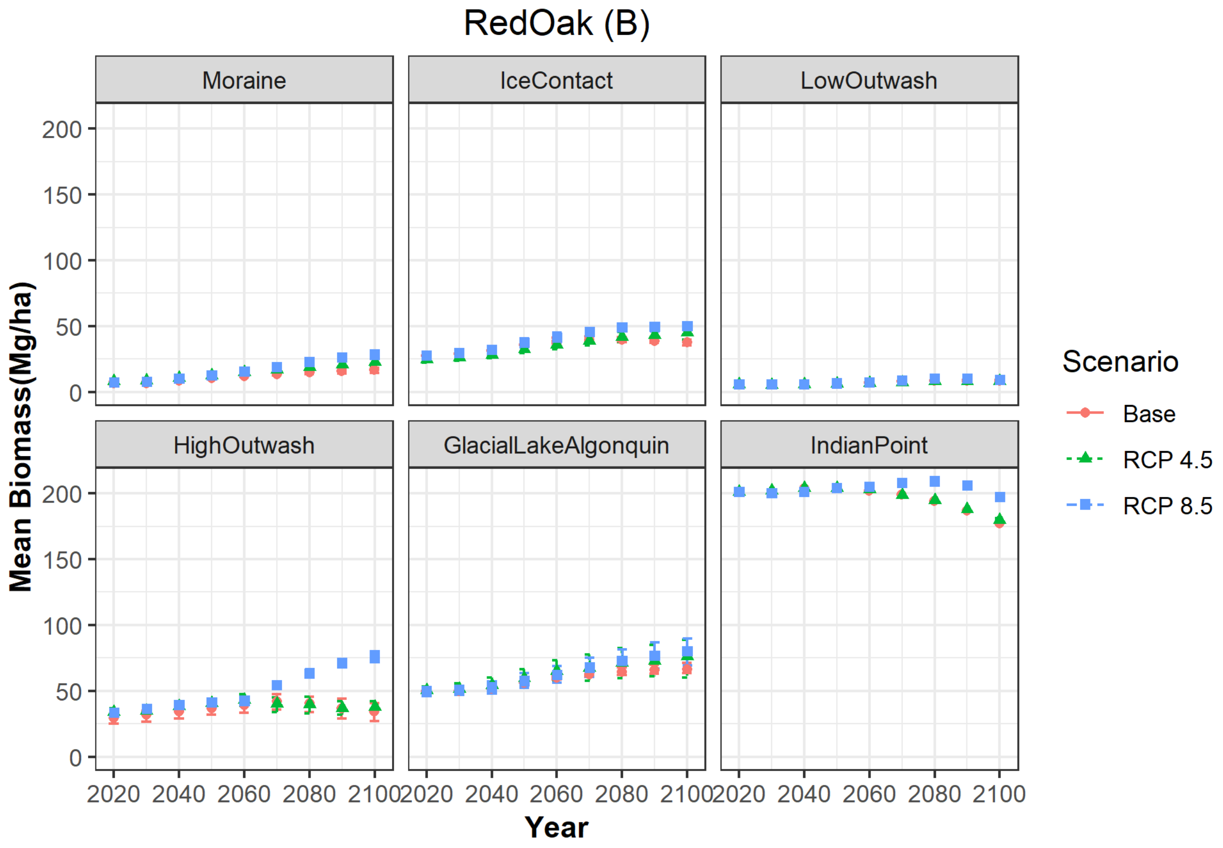
RCP 4.5
RCP 8.5


RedOak (B)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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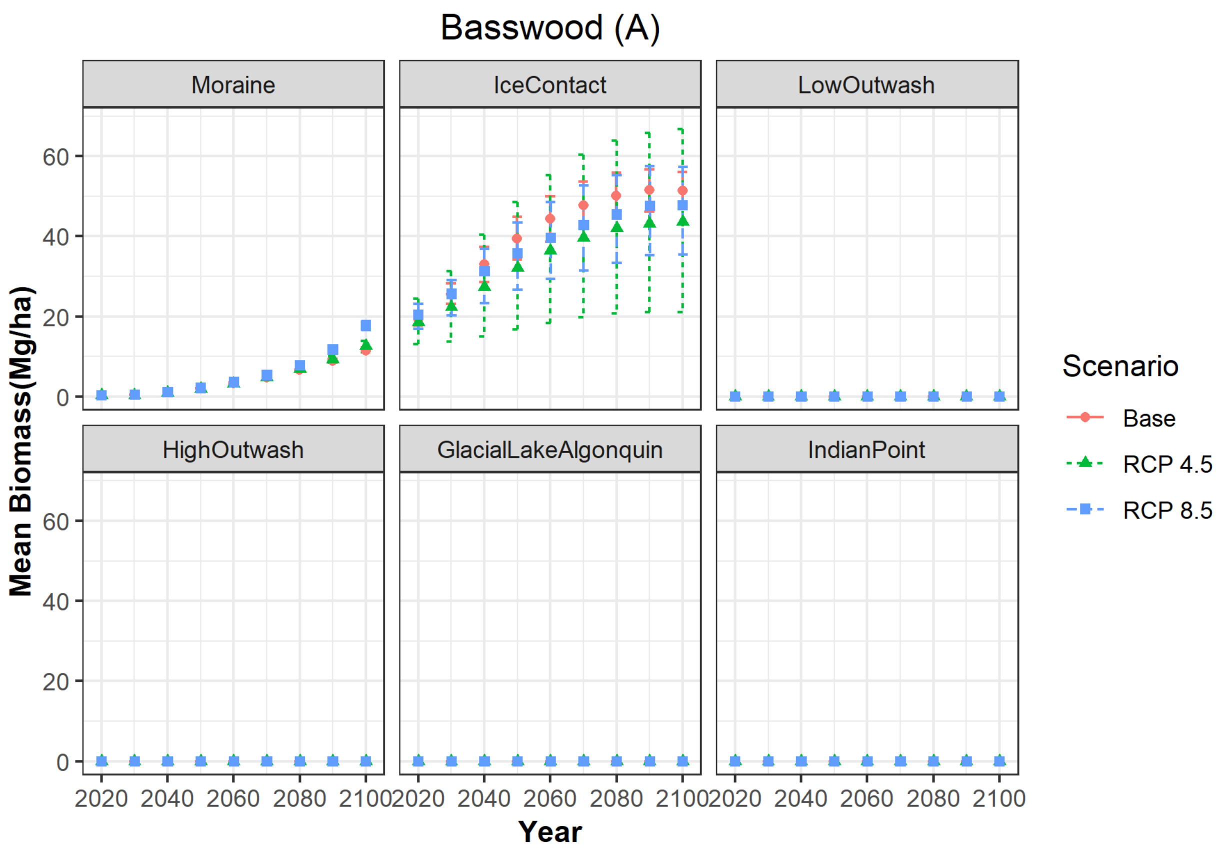
Scenario
Base
RCP 4.5
RCP 8.5


Basswood (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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Scenario
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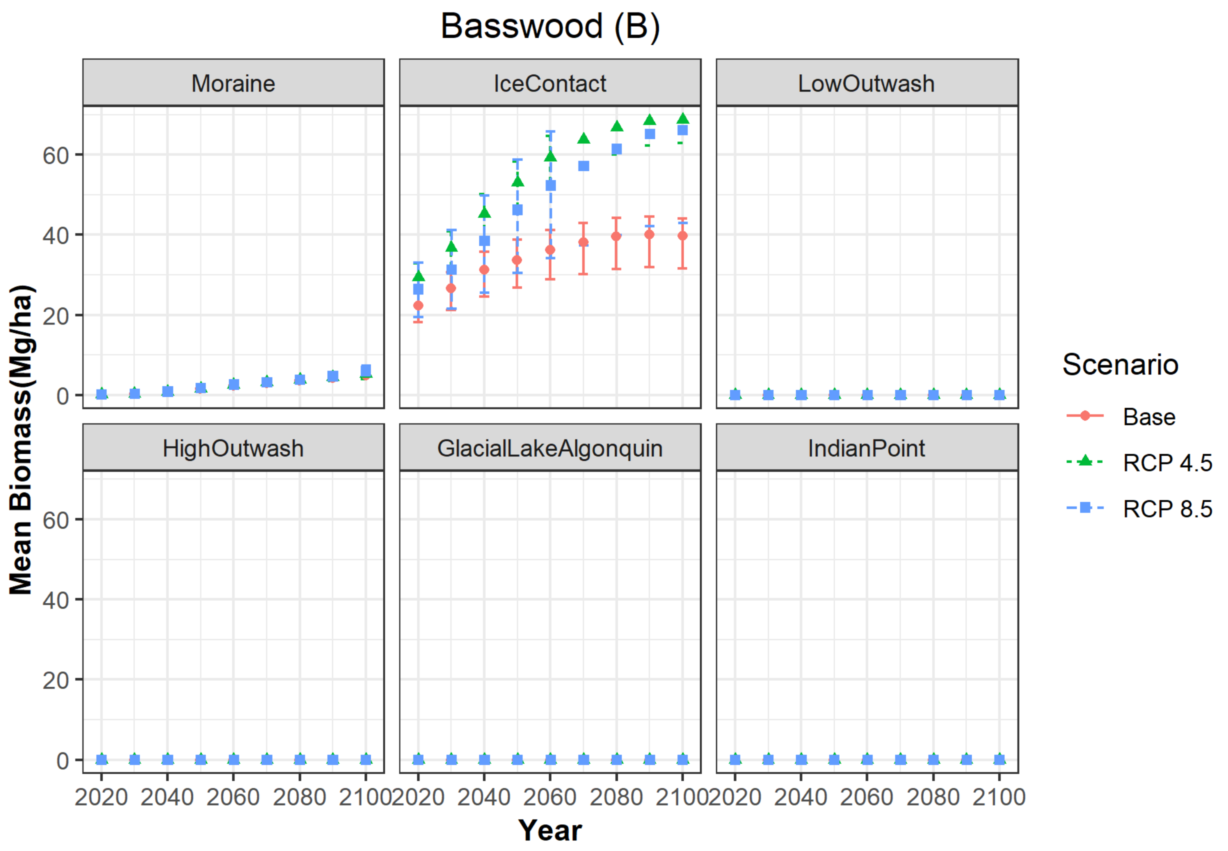
RCP 4.5
RCP 8.5


Basswood (B)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
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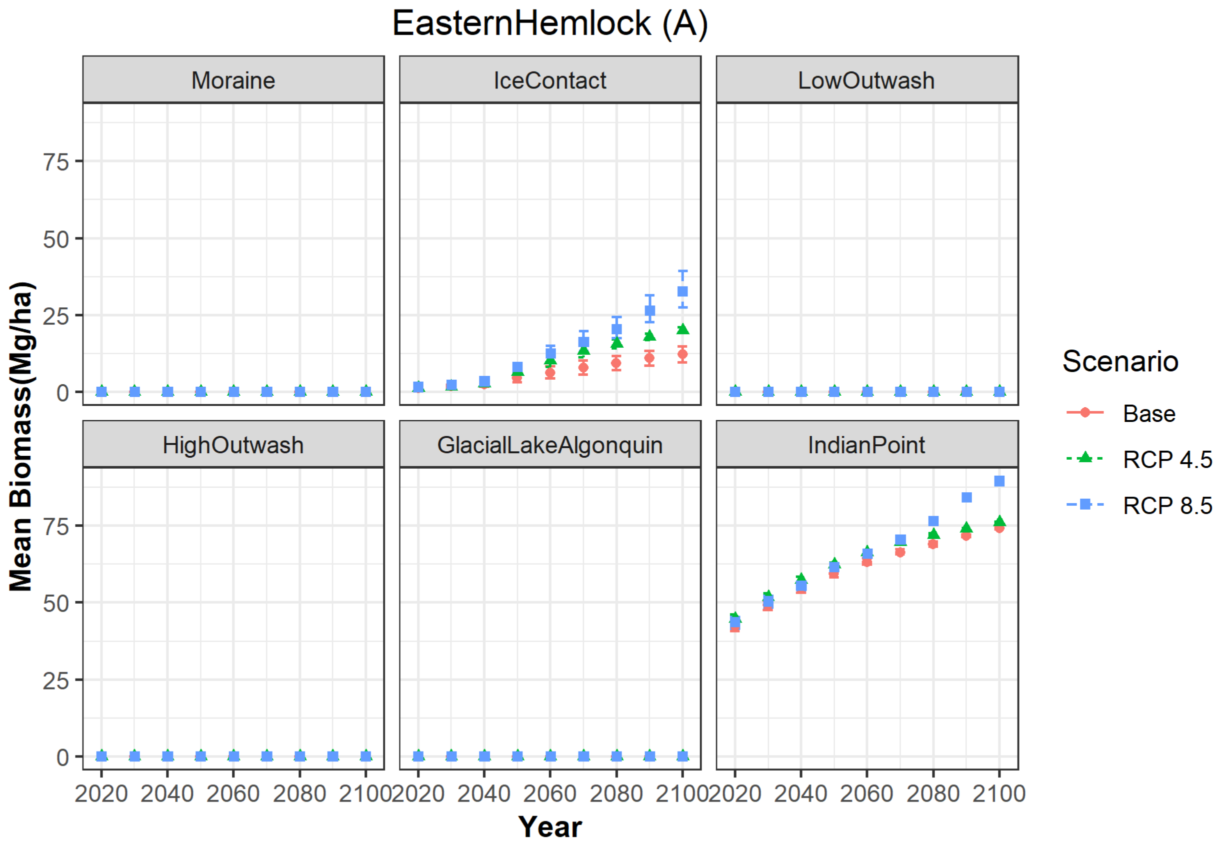
Scenario
Base
RCP 4.5
RCP 8.5


EasternHemlock (A)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
0
25
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Year
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2040
2060
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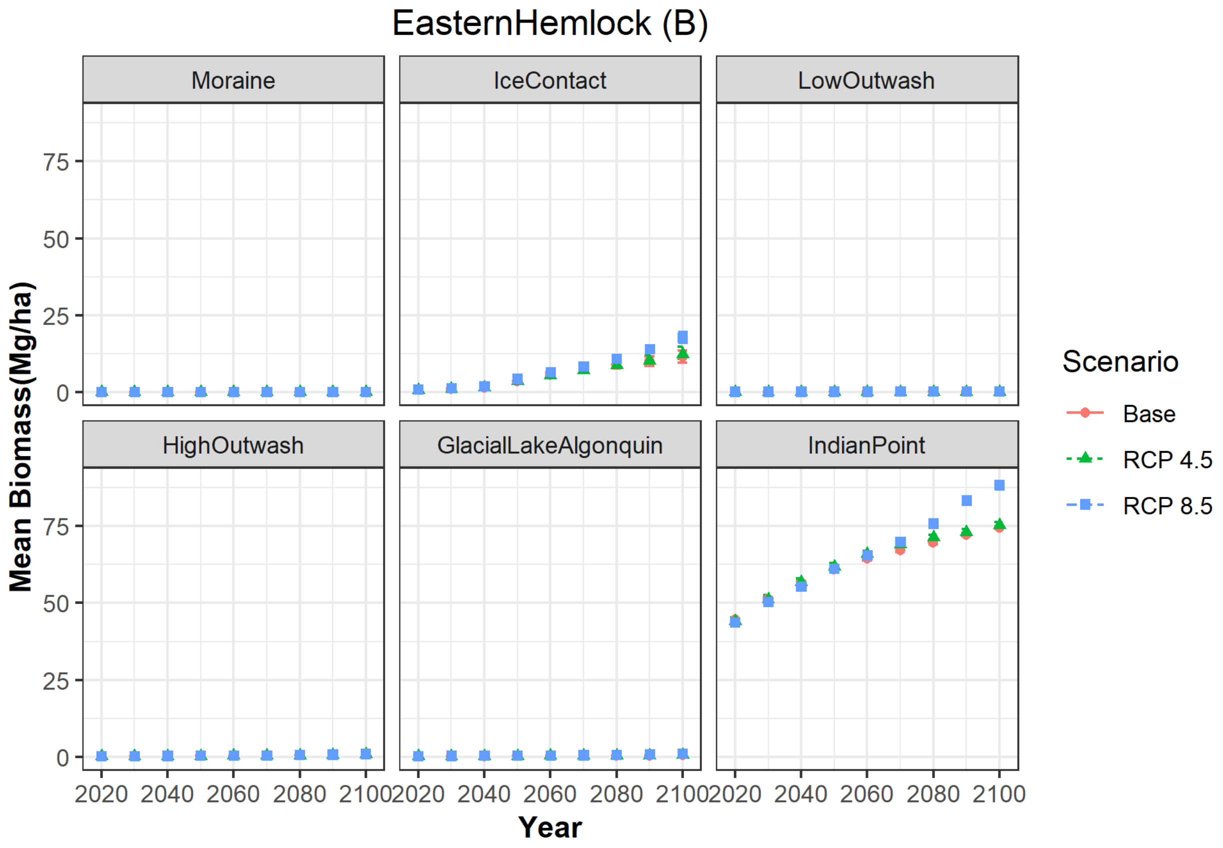
2100
Scenario
Base
RCP 4.5
RCP 8.5


EasternHemlock (B)
Moraine
IceContact
LowOutwash
HighOutwash
GlacialLakeAlgonquin
IndianPoint
Mean Biomass(Mg/ha)
0
25
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75
Year
2020
2040
2060
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Scenario
Base
RCP 4.5
RCP 8.5

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