Climate change threatens the sustainability of current timber harvesting practices across a latitudinal gradient in Siberia

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Code availability -LANDIS-II is open-source and available at www.landis-ii.org.

Data availability - Data inputs for this study are available at https://github.com/LANDIS-II-Foundation/Project-Siberia/tree/main/Gustafson_etal_Harvest.

Abstract

The boreal forests of Eurasia form the largest contiguous terrestrial biome in the world, providing numerous ecosystem functions and services for human societies. Temperatures are increasing most rapidly in high northern latitudes, altering tree growth and competition dynamics, and modifying disturbance regimes. The effect of these cumulative changes on the ecosystem functions provided by boreal forests is difficult to predict. We used the process-based LANDIS-II forest landscape model to evaluate how climate change and timber harvesting will interact to alter the production of ecosystem functions and services in boreal forests on three study areas across a large latitudinal gradient (11°) in central Siberia. We found that the relative importance of wood harvesting as a disturbance type varied depending on latitude and its impact was always far less than that of fire. Moderate climate change increased the availability of wood for harvest in the northern landscape, but wood availability declined in the southern landscapes under any amount of climate change likely because of an increase in the frequency of fire that kept forests too young for harvest. Modest climate change (RCP6.0) increased productivity and the storage of carbon in all landscapes but severe climate change (RCP8.5) reduced both in the southernmost landscape. Harvesting as a specific driver of change in these boreal forests is likely to be relatively minor except as a forest fragmentation process. Our results provide compelling evidence that *status quo* forest management in these landscapes is likely not sustainable, suggesting that climate-smart forestry will be needed.

Introduction

The boreal forests of Eurasia form the largest contiguous terrestrial biome in the world, and they contain 30-50% of the world's forest carbon stocks (Pan et al. 2011). Boreal forests provide a large and critical carbon sink, with Russian forests alone sequestering 0.21±0.09 PgC yr^{-1} in the form of new woody biomass (Shvidenko et al. in review). Russia's boreal forests, with their ~68 billion m^3 of growing stock volume (Schepaschenko et al. 2021; Filipchuck et al. 2022) represent the largest potential source of commercial wood products in the world. These vast forests also provide other critical ecosystem functions (*sensu* Manning et al. 2018) in the form of biotic diversity of both plants and animals, above- and below-ground carbon storage, water quality and quantity, and many others.

At a global scale, 60% of boreal forests are designated as managed, ranging from 35% in Canada (Burton et al. 2010; Vernier et al. 2014) to 58% in Russia (Federal Agency of Forest Service 2009) and 90% in Fennoscandia (Burton et al. 2010). Management intensity is generally low in Canada and Russia and higher in Fennoscandian forests. Managed forests are an important source of wood for commercial purposes because of their abundance and quality, and also for heating fuel because of their proximity to dispersed demand centers. In boreal Russia, both harvesting and forest protection have dropped substantially since the collapse of the Soviet Union (FAO 2012; State Program of the Russian Federation 2020). Also, despite existing laws and regulations, up to 20% of current logging is carried out illegally (FAO 2012), often with overharvesting of high-value (large) stems in the most accessible stands (Newell and Simeone 2014). More recently, the socio-economic pressure to harvest forests is growing in currently unharvested areas throughout Eurasia (Shvidenko et al. 2007), which could compromise forest

sustainability, alter successional dynamics and forest composition, and interact with climate change and other disturbances in ways that are not fully understood (Gustafson et al. 2011).

Temperatures are increasing especially rapidly in high northern latitudes (Leskinen 2020; IPCC 2021), resulting in modified disturbance regimes (Gauthier et al. 2015) and greater thawing of permafrost in summer (Chapin et al. 2010). Between 1976 and 2021, Russia experienced warming (+0.49◦C/decade) that was more than twice that of the global average, with even higher rates recorded in central Siberia in spring (+0.84 ◦C/decade) (Roshydromet 2022). Precipitation also increased modestly (+84 mm/month/decade), but perhaps insufficiently to meet increased water demand by plants. Elevated temperatures result in increases in active layer thickness in permafrost areas, lengthening of growing seasons, and favorable temperatures for photosynthesis are becoming more likely in late June/early July when daylength is the longest. However, weather extremes are becoming more pronounced and destructive, and may result not only in more heat waves, but perhaps in more cold-killing events, at least in the next few decades (Gustafson et al. 2020). In the recent past, heat waves producing catastrophic fires and increasing pest disturbances are the most common modification of historical disturbance regimes in Siberian forests (Shvidenko and Schepaschenko 2013; Ponomarev et al. 2021).

Tree species will be differentially stressed or favored by altered temperature, precipitation, permafrost hydrology, and CO_2 fertilization, depending on their physiological traits, thus altering competitive interactions and biotic equilibria. Current species will be better able to survive in locations to the north and perhaps less able to compete in locations near the southern edge of their current range. The movement of climate isotherms (climate velocity) is likely to far outpace the ability of tree species to disperse as needed to maintain populations (biotic velocity), especially at high latitudes (Dial et al. 2016). Past attempts to predict how climate change will

affect boreal forests have not adequately captured interactions among multiple disturbances (i.e., wind, insects, fire, climate extremes and harvest), seed dispersal and climate change. Additionally, disturbances may become more frequent and more intense, altering forest composition to favor better adapted species, and potentially shifting age class distributions (Shvidenko and Schepaschenko 2013; de Groot et al. 2013). Shifts in forest composition and age class structure may threaten the supply of merchantable timber given current utilization standards, milling infrastructure and product markets, as well as changes in productivity and carbon storage.

These integrated effects of changing climate, harvesting and natural disturbances may also have repercussions for landscape structure, including patchiness and wildlife habitat. Fragmentation could be increased by changes in harvesting in response to increased productivity or by more prevalent natural disturbances and climate-induced dieback events. These changes may have complex effects on ecosystem functioning, including feedbacks to productivity (e.g., by edge effects and microclimatic buffering), resilience to future disturbances, and wildlife habitat suitability for species such as caribou (Mallory and Boyce 2018) and Siberian flying squirrels (Hof et al. 2012).

Most published studies predicting the response of boreal ecosystems to climate change used dynamic global vegetation models (DGVMs), bioclimatic envelope models, or data assimilation systems (e.g., Tchebakova et al. 2016; Bloom et al. 2016; Lòpez-Blanko et al. 2019). These models typically have a coarse spatial resolution (e.g., 0.5 degrees lat/long) and represent vegetation as proportional occupancy by plant functional types (not species). The strength of DGVMs is their use of highly mechanistic plant growth algorithms based on physical and physiological first principles, which produce robust predictions of growth and competition under

the novel conditions of the future. Their weakness is their extremely limited spatial specificity, which makes it difficult to specifically account for important regional ecological processes with an important spatial component, such as harvesting, most natural disturbances, and seed dispersal and establishment. It has been shown that most studies conducted for Russian territories using DGVMs substantially overestimated heterotrophic respiration, therefore underestimating net carbon storage in forested ecosystems (Shvidenko and Schepaschenko 2014). Our study explored how models with finer resolution may generate results (e.g., timber harvest impacts on ecosystem goods and services) not available from coarse resolution models.

Process-based forest landscape models (FLMs) are a powerful tool to predict future landscape dynamics under novel conditions without historical analog. They feature a spatially interactive representation of landscapes as a grid of cells with a resolution that typically falls in the range of 10-250 m. Their primary strength is simulation of spatially contagious disturbances that interact with abiotic and vegetation characteristics of the landscape, the dispersal of propagules from sexually mature cohorts, and the establishment of new cohorts as a function of their tolerance of the conditions on the grid cell. Their weakness is a (relatively) limited spatial extent (typically $<10^7$ ha) and somewhat less mechanistic simulation of tree growth and competition, both required by their spatial resolution and the spatially explicit nature of their algorithms. However, one of their strengths is the ability to simulate a wide range of forest management activities targeted to specific species on specific parts of the landscape, a capability that is quite limited in DGVMs.

In this study we used the LANDIS-II FLM to evaluate how climate change and disturbances may alter timber harvesting in boreal forests across a large latitudinal gradient in central Siberia. This location is relatively under-studied and such a large latitudinal gradient is not forested

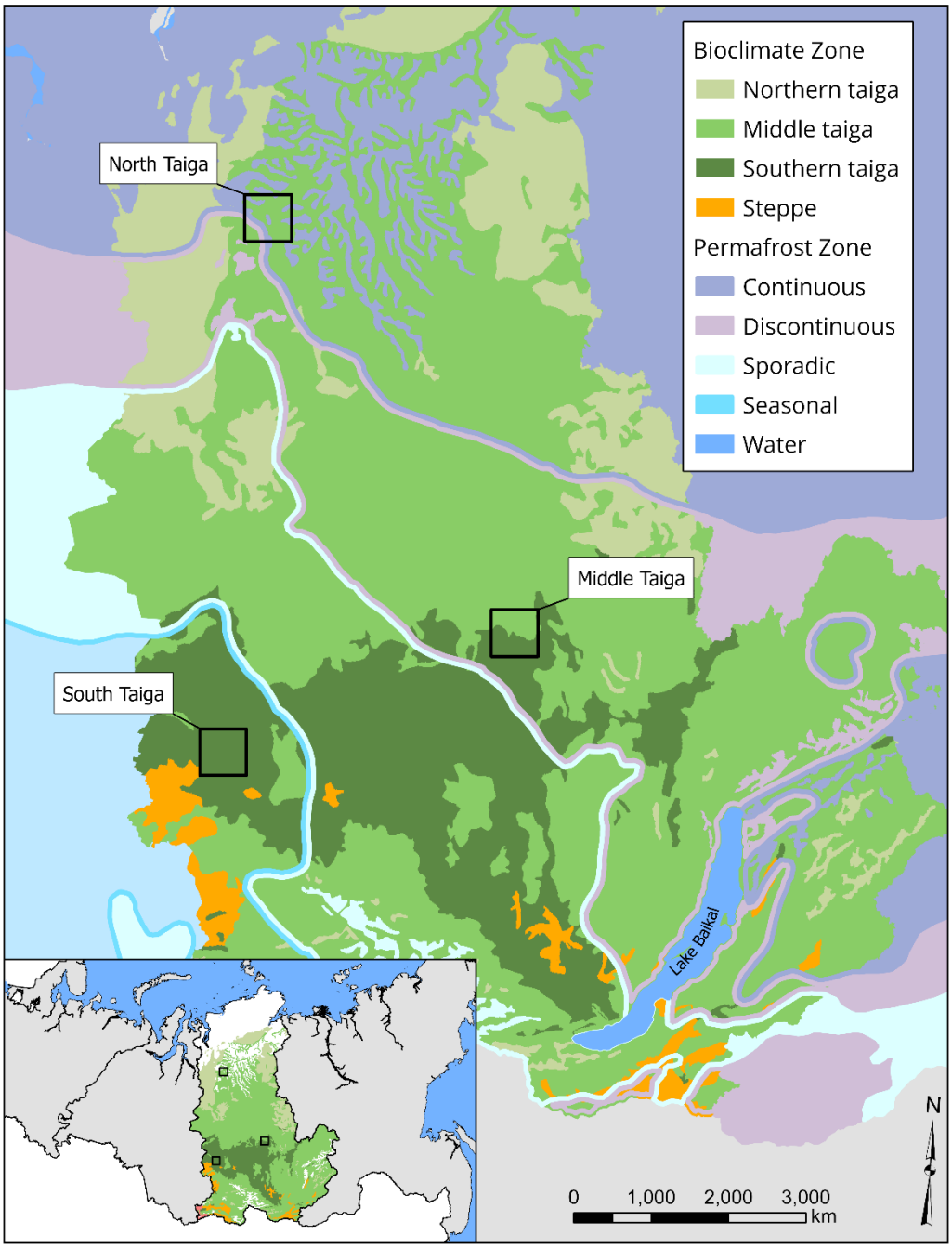
(without mountains) on other continents. We tested three specific hypotheses. H1: climate change will increase the amount of tree biomass, achieved primarily by the northward expansion of productive forests and enhanced growth resulting from CO_2 fertilization. H2: Total annual net primary productivity will increase because both climate change (including CO_2 fertilization and lengthened growing seasons) and the general reduction of forest age by harvesting will increase growth rates. H3: climate change will increase the amount of timber available to harvest (i.e., more rapid growth) and therefore allow an increase in the amount of harvesting, increasing fragmentation.

Methods

We used the LANDIS-II FLM to conduct a factorial simulation experiment that varied latitude (three landscapes), climate (three climate scenarios) and harvesting (two contrasting regimes) to project landscape responses of ecosystem functions.

The latitude factor was implemented using three study landscapes along a broad latitudinal gradient in Siberia (Fig. 1) located within 96-102^o East and 57-67^o North, each 1 million ha in size. The northernmost site (Northern taiga, 67^o N) is currently mostly unharvested, and is composed primarily of light coniferous forests (larch, Scots pine) and arctic shrubs and grasses on continuous permafrost (i.e., entire area has permafrost). The middle site (Middle taiga 59^o N) is currently moderately harvested, and composed primarily of dark coniferous forests (spruce, Siberian pine, fir) on discontinuous permafrost. The southernmost study site (Southern taiga, 57^o N) is currently heavily harvested and is composed of a mix of deciduous and conifer species in a zone at risk of loss of forests to grasslands at a biome ecotone (forest-steppe). The location of this site was chosen to avoid the confounding climatic effects of the high-elevation Sayan Mountain range to the southeast.

Initial tree communities for each cell of each study area were created using Siberian plot and tree data from an Integrated Land Information System (Schepaschenko et al. 2017, 2018). Species composition within plots was estimated from growing stock volume of each species, and ages of those species were assigned by randomly imputing from the trees in the tree database sharing site characteristics (bioclimatic zone, ecoregion, site index, stand age, dominant species) of the plot. Specific species cohorts and ages were then imputed to each 2.25 ha-cell by randomly sampling from plots with similar characteristics (bioclimatic zone, ecoregion, site index, stand age, dominant species). We initialized non-arboreal species (i.e., shrubs, mosses, and grasses) based on a suite of ecologically relevant rules (e.g., riparian species, species associations) using expert judgement and published information (e.g., Krivobokov et al. (2020), Mukhortova et al. (2020), Gudilin (1987)). The abiotic conditions of each cell were assigned based on a map of bioclimatic zones (Stolbovoi and McCallum 2002), and a map of ecoregions (Schepaschenko et al. 2011, Shvidenko and Schepaschenko 2014).



150

151 **Fig. 1** Location of the three study sites across a large latitudinal gradient in central Siberia,

152 showing permafrost and bioclimate zones (Stolbovoi and McCallum 2002). Inset map shows the

153 study context within the Russian Federation

154 The simulation experiment was conducted using LANDIS-II v7 (Scheller et al. 2007), which
155 simulates growth, mortality (including by disturbance), and reproduction of tree species-age
156 cohorts (i.e., not individuals) on grid cells that interact spatially through seed dispersal and
157 contagious disturbances. LANDIS-II represents vegetation as species-age cohorts, and their
158 growth, competitive behavior, reproduction, and response to disturbance is driven by life history
159 traits (Table 1). LANDIS-II has previously been used in Siberia to study the relative effects of
160 climate change, timber harvesting, and insect outbreaks on forest composition, biomass and
161 landscape pattern in central Siberia (Gustafson et al. 2010, 2011, in review).

162

163 Table 1. Selected LANDIS-II parameters for the species simulated. Parameters represent typical
164 cohort life-history traits, derived from many Russian sources (e.g., Chertovsky et al. 1983;
165 Osawa et al. 2010). Non-tree species are indicated by *.

Species common name	Scientific name	Longevity (yrs)[1]	Sexual maturity (yrs)	Prob. of re-sprouting[2]	Post-fire reproduction
Larch	*Larix spp.*	300	12	0.0	Seed
Siberian spruce	*Picea obovata*	220	25	0.0	Seed
Stone pine	*Pinus sibirica*	280	35	0.0	Seed
Siberian fir	*Abies sibirica*	180	40	0.0	Seed
Scots pine	*Pinus sylvestris*	220	15	0.0	Serotiny
Silver birch	*Betula pendula*	120	10	0.5	Resprout
Eurasian aspen	*Populus tremula*	100	7	0.9	Resprout
Alder*	*Alnus fruticosa*	70	10	0.9	Resprout
Willow*	*Salix spp.*	65	10	0.9	Resprout
Dwarf birch*	*Betula nana*	120	30	0.9	Resprout
Sphagnum*	*Sphagnum spp.*	220	20	0.8	Seed
Arctic grass*[3]	Pseudo-species	500	5	0.95	Resprout
Steppe grass*[4]	Pseudo-species	500	2	0.95	Resprout

166 [1] Typical longevity of cohorts of the species (not unusually long-lived individuals)

[2]Probability of sprouting after disturbance

[3] Arctic grass was parameterized as a pseudo-species representing typical tundra ground cover vegetation composed of a mixture of grasses, lichens and mosses

[4] Steppe grass was parameterized as a pseudo-species representing ground cover typically found in steppe ecosystems

We used a relatively mechanistic LANDIS-II succession extension (PnET-Succession v.5.1) that operates at a monthly time step and relies heavily on physiological first principles (De Bruijn et al. 2014; Gustafson et al. 2023a). PnET-Succession is based on the "big leaf" PnET-II model (Aber et al. 1995), and simulates monthly photosynthesis for each cohort using physiological first principles (Gustafson 2013). It tracks soil water at the grid-cell level using a bulk-hydrology model based on precipitation, loss to foliage interception, evaporation, soil texture, runoff, and percolation out of the rooting zone, and consumption by species cohorts (transpiration). Depth to permafrost, (computed in summer months) is a function of temperature, snow cover, vegetation and soil thermal conductivity (Abels 1892; Sitch et al. 2003; Beer et al. 2007; Jonas et al. 2009), which determines maximum rooting depth and leaching (see Gustafson et al. (2020) for modeling details). Cohort biomass is a proxy for relative access to light, and the effect of soil moisture depends on each species' waterlogging and drought tolerance (parameters H1-H4). When water is not limiting, the amount of photosynthesis for a given species cohort increases with available light (dependent on canopy position, leaf area and shade tolerance (half-saturation point)), atmospheric CO_2 concentration and foliar N, and decreases with age and departure from optimal temperature for photosynthesis. Photosynthates are allocated to pools of

189 foliage, wood, roots and reserves. PnET-Succession accounts for respiration such that growth
190 respiration depends on temperature and moisture stress, while maintenance respiration depends
191 on temperature and biomass. Shrub species can compete with trees, mimicking observed
192 dynamics at all sites. We also simulated grasses, lichens, and mosses. Given the arrival of seeds
193 by dispersal, establishment probability in PnET-Succession is proportional to photosynthetic
194 rates calculated for that species at ground level and can vary dynamically through time as a
195 function of light and water availability. PnET-Succession can output maps and tables of many
196 cohort state variables for each landscape grid cell through time (Gustafson et al. 2024).
197 Calibration of PnET-Succession parameters is described in Williams et al. (2023), and selected
198 parameter values are given in Table 2. All LANDIS-II parameters are available in the
199 Supplement.

200 Table 2. Selected PnET-Succession parameters for each species, synthesized from many Russian
201 sources (e.g., Chertovsky et al. 1983; Osawa et al. 2010). Non-tree species (indicated by *) were
202 parameterized as pseudo-species calibrated to appropriately burn and consume water and light.

Species	FolN (% by mass)	SLW Max (g/m^2)[1]	HalfSat[2] (μmol/ m2/s)	H1[3] (m)	H2[3] (m)	H3 & H4[3] (m)	Leaf OnMinT (°C)[4]	PsnTMin (°C)[5]	PsnTOpt (°C)[5]	Cold Tol (°C)[6]
Larch	2.3	70	275	-2.4	1	149	1.3	0	24	-65.2
Spruce	1.2	125	150	-1.5	1	144	1.4	0.4	26	-64
Dwarf birch*	2.2	70	265	-4	1	144	1.2	-0.4	17	-67
Stone pine	1.35	185	245	-3	2	151	1.5	1.0	26	-63
Fir	1.15	110	134	-3	2	144	1.6	0.7	26	-61
Scots pine	1.35	215	260	-2.3	1.5	157	1.4	0.7	26	-63
Birch	2.8	65	245	-1	1.2	146	1.7	1.5	28	-61
Aspen	2.7	68	234	-1	1.2	149	1.7	1.5	28	-57.5
Alder*	2.3	60	220	-4	1	3.4, 5	1.4	1.0	26	-66.3
Willow*	2.3	60	220	-4	1	3.4, 5	1.7	1.5	27	-67

Sphagnum*	2.1	120	130	-50	0	3.4, 15	1.4	0.4	24	-65
Arctic grass*	2.1	105	222	-1	0	151	1.2	-0.4	17	-68
Steppe grass*	2.3	90	275	-3	1	170	2.6	2.0	30	-50

[1] Maximum specific leaf weight determines leaf thickness and is used to compute cohort LAI.

[2] Half saturation point; lower values represent greater shade tolerance.

[3] H1=soil water potential (absolute values of meters pressurehead) above which photosynthesis stops due to waterlogging (negative values allow some photosynthesis in standing water); H2=water potential above which photosynthesis slows due to waterlogging; H3=water potential below which photosynthesis slows due to drought; H4=water potential below which photosynthesis stops due to drought. H3 is usually equal to H4, resulting in instantaneous water starvation when soil water potential drops below H3. Exceptions to this show two values (H3, H4) in the table.

[4] Mean monthly temperature above which leaves and photosynthesis are active. Dynamically determines growing season length.

[5] Photosynthesis temperatures are given in terms of mean monthly daytime temperature ((Tmax+Tavg)/2).

[6] Coldest temperature the species can survive.

The climate factor had three levels (Historical, Intermediate, Shared Socioeconomic Pathway 585 (SSP585)). Because an intermediate SSP climate scenario was not available for our study areas at the time of simulation, we generated one as described below. For the Historical climate treatment, we used the GSWP3 climate product for the years 1980-2014 (Compo et al. 2011).

The extreme climate treatment (IPCC 2021) was derived from the CESM2-WACCM SSP585 product (Rodgers et al. 2021) for the years 2015-2300. These two climate scenarios were bias-corrected (downscaling bias) to produce a smooth transition between past weather streams (1901-2015) used for spinup and future weather streams. The projections were extended beyond the year 2100 by altering the value of each variable into the future by the slope (through time) of that variable during the last 30 years of the projection. The purpose of the Intermediate climate treatment was to allow evaluation of the response variables under a climate that was midway between the extremes, and a hypothetical Intermediate climate stream was generated by computing the average of each climate variable (through time) between the Historical and SSP585 scenarios. We used the LANDIS-II climate library (v.4.2, Lucash and Scheller 2021) to ensure that each LANDIS-II extension received its required weather inputs from the same source at the same time.

The Harvesting experimental factor had two levels (current Harvest regime, No Harvest). Timber harvesting was simulated using the Biomass Harvest extension v.4.5.1 (Gustafson et al. 2000). This extension simulates removal of cohort biomass (including partial removal of individual cohorts) caused by timber harvest activities and links to the fuel extension to account for logging slash. Harvesting of each forest type was simulated using a unique prescription informed by the Forest Code of the Russian Federation (see https://www.garant.ru/products/ipo/prime/doc/74983487) and expert knowledge of local practice. The Harvest extension regulates cutting rates by rotation length rather than Annual Allowable Cut or wood demand, and rotation lengths were estimated from expert knowledge of current cutting practices. Illegal harvest of each type was simulated as clearcuts, at a rate varying between 5 and 20% of legal harvest (Table 3). The northern study area is comprised of sparse

245 forests that are expected to become more productive and dominant with climate change. They are
246 managed by a "Protective" silvicultural strategy specified in the Russian Forest Code, which
247 generally uses longer rotations, avoids clearcuts and leaves more residual (uncut) forest after
248 harvesting (Table 3). The southern two (more productive) study areas are managed by an
249 "Exploitative" silvicultural strategy, with shorter rotations and clearcutting methods, leaving less
250 residual forest behind. Most harvest prescriptions involve two stand entries; the first entry
251 applies a thinning cut, followed some decades later by a mature tree removal cut (either single-
252 tree selection cutting or clearcut) (Table 3). Initial harvest rates were set to achieve the desired
253 rotation length for each type based on the areal abundance of each harvested species in the initial
254 condition maps. After the first rotation, harvest rates responded to the availability of each species
255 through time. The Harvest extension applies prescriptions to spatial units (stands), but no
256 technique to generate stand boundaries on imputed initial conditions maps is yet available, so a
257 grid of arbitrary stand boundaries was imposed on each landscape. Stands in the northern
258 landscape (Protective harvest rules) were 18 ha in size (600 x 300 m) and in the southern two
259 landscapes (Exploitative rules) stands were 45 ha in size (750 x 600 m). Harvests were not
260 simulated in the parts of each landscape that are officially set aside from harvesting, although the
261 total amount of such areas was quite small. The Harvest extension estimates a forest type at each
262 time step for each stand based on the composition of the cells in the stand.

263 Table 3. Harvest regimes (prescriptions) for each forest type (as specified for the Harvest
264 extension) by Russian management system (Exploitative or Protective). Some harvest methods
265 use two entries per rotation (each with a different cutting strategy, denoted by a "/").

Forest type	Harvest method	Min. age (yrs)	Min. time between	Nominal rotation	Residual (uncut	Adja-cency	Stand ranking method[2]

			entries (yrs)	length (yrs)	stand area) (%)	limit (yrs)[1]	
Exploitative management system[3]							
Larch	Thin/clearcut	60	60	120	10	5	Oldest
Spruce	Thin/clearcut	60	60	120	10	5	Oldest
Fir	Thin/clearcut	60	60	120	10	5	Oldest
Scots pine	Thin/clearcut	60	60	120	10	5	Oldest
Stone pine	Selection	60	38	NA	0	0	Oldest
Aspen/birch	Clearcut	70	70	70	10	2	Oldest
Protective management system [4]							
Larch	Thin/select	80	80	160	12.5	5	Oldest
Spruce	Thin/select	70	70	140	12.5	5	Oldest
Fir	Thin/select	70	70	140	12.5	5	Oldest
Scots pine	Thin/select	80	80	160	12.5	5	Oldest
Stone pine	Selection	60	38	NA	0	0	Oldest
Aspen/birch	Clearcut	70	70	70	10	2	Oldest
Illegal[5]							
Stone pine	High-grade	100	0	NA	0	0	Value
All others	Clearcut	90	0	NA	0	0	Value

[1] All adjacent stands must be at least this old for the focal stand to be eligible for harvest.

[2] Determines the order in which eligible stands for the forest type prescription are harvested. "Value" ranks stands by economic value.

[3] Exploitative: More aggressive harvest system applied in the two southern-most study areas.

[4] Protective: Less aggressive harvest system applied in the northernmost study area.

[5] Illegal: Not officially sanctioned or conducted according to Russian Forest Code. Harvest rules generated from expert knowledge. Implemented at a rate of 5% of legal harvest in the northern study area and 20% in the southern two study areas.

Because seed dispersal was not possible from outside each landscape, we used the Harvest extension to introduce more southerly species (not initially extant in the landscape) along the southern border of each landscape once each decade to simulate colonization. These cohorts

278 survived only when climate conditions (cold extremes) permitted and their ability to then
279 colonize the landscape was determined by seed dispersal and competitiveness with existing
280 vegetation, mediated by disturbances. This mimics the behavior of colonization processes that
281 our model was unable to simulate.

282 Natural disturbances (fire, insects, and wind) were considered chronic background
283 disturbances (parameterized the same for all treatment combinations), although fire and insects
284 nevertheless responded to their climate and vegetation drivers. This is not a confounding of the
285 climate treatment effect, but rather a complete accounting of the climate effect because some of
286 these disturbances are partially driven by climate and they are a powerful driver of forest
287 succession (Liang et al. 2023) in this biome. Fire was simulated by the BFOLDS (Boreal Forest
288 Landscape Dynamics Simulator) Fire Regime extension (v2.2, Ouellette et al. 2022) because a
289 BFOLDS wildfire regime is an emergent property of climate and fuel (live and dead vegetation),
290 desirable because future functioning of these ecosystems is not anticipated to have the historical
291 analog needed to parameterize other extensions. Parameters were adjusted under historical
292 climate to match empirical observations of fire rotation intervals, fire size and area burned
293 (Schepaschenko et al. 2011; Shvidenko and Schepaschenko 2014) as described by Williams et al.
294 (2023). Fuel type for each cell (needed by BFOLDS) was estimated using the Dynamic Fuels
295 extension (v3.0, Sturtevant et al. 2009). Defoliation disturbance by the major insect defoliator
296 (Siberian silk moth) was simulated with the Biological Disturbance Agent extension (v4.1.0,
297 Sturtevant et al. 2004). This extension simulates the mortality of tree cohorts caused by insect
298 defoliators using relationships between insect tree species host abundance and temperature and
299 drought to simulate defoliation outbreaks and was calibrated as described in the Appendix. Wind
300 disturbance was simulated using the Base Wind v3.0 extension (microbursts, Mladenoff and He

301 1999) and the Linear Wind v1.0 extension (derechos and tornadoes, Gustafson et al 2016), using
302 parameters from other studies in Siberia (Gustafson et al. 2010) and N. America (Lucash et al.
303 2017). Because we had no robust way to estimate future wind regimes under climate change,
304 they were held constant.

305 The experimental landscapes were represented with a grid cell resolution of 150 m. We
306 generated four replicates of each factorial combination, where each replicate varied the
307 stochasticity of the model (via random number seed); climate and initial conditions did not vary
308 among replicates. We simulated 280 years for each replicate to ensure at least one complete
309 rotation for each forest type and allow sufficient time for forests to respond to the experimental
310 treatments. To quantify the effect of the experimental treatments on ecosystem functions and
311 services, we extracted relevant state (response) variables from model outputs every 10 simulated
312 years (Table 4). Outputs were reclassified using the Biomass Reclassification Output extension
313 (v3.2, (Scheller 2019) to create maps of forest type (Table 5)

314

315 Table 4. Response variables used to quantify the effect of the experimental treatments on
316 ecosystem multifunctions. Most variables were computed as a mean value per cell every 10
317 years.

Response variable	Description	Units
Area occupied by each tree species	Species composition	km^2
Area harvested by species	Areal extent of all harvested cells	ha
Biomass harvested	Live wood biomass killed by harvest activities	Mg/m^2
% contemporary harvest rate	Ability to sustain harvest rates	percent
Mean carbon storage	Mean live above-ground biomass	g/m^2
Annual net primary productivity	Mean productivity of all species	Mg/ha/yr
Core area	Area of forest >300m from an opening	ha

Forest patchiness	Mean size of forested patches.	Ha

Table 5. Forest type classification as typically used by Eurasian forest managers.

Forest Type	Dominant species	Reclassification for fragmentation	Notes
Dark conifer	*Abies sibirica Picea obovata Pinus sibirica*	Forest	Generally shade tolerant
Light conifer	*Pinus sylvestris Larix spp.*	Forest	Shade intolerant
Deciduous	*Populus tremula Betula pendula*	Forest	Limited cold tolerance
Wetland forest	*Alnus fruticosa Salix spp. Sphagnum spp.*	Open	Limited to supersaturated soil
Shrub	*Betula nana*	Open	Very cold tolerant
Arctic ground vegetation	Arctic grass/lichen	Open	Extremely cold tolerant
Steppe grass	Steppe grass	Open	Limited cold tolerance
Inactive cell	None (Inactive, typically water)	Open	Cell not simulated

To evaluate our hypotheses, we relied primarily on graphical depictions of trends (with 1 STD uncertainty envelopes) in response variables by treatment through time, interpreting treatment effects as significant when uncertainty envelopes did not overlap after 100 years. This approach is generally superior to statistical tests for simulation modeling studies because models can readily generate many observations that may not include all sources of uncertainty (White et al. 2014). Accordingly, we limited replicates (N=4).

Results

Timber harvest

The extraction of wood (timber harvest) was quantified in terms of area harvested and biomass harvested (reported as biomass of living cohorts killed; includes slash and waste). The area harvested was generally less than the area burned and was much less under climate change

(Fig. 2).

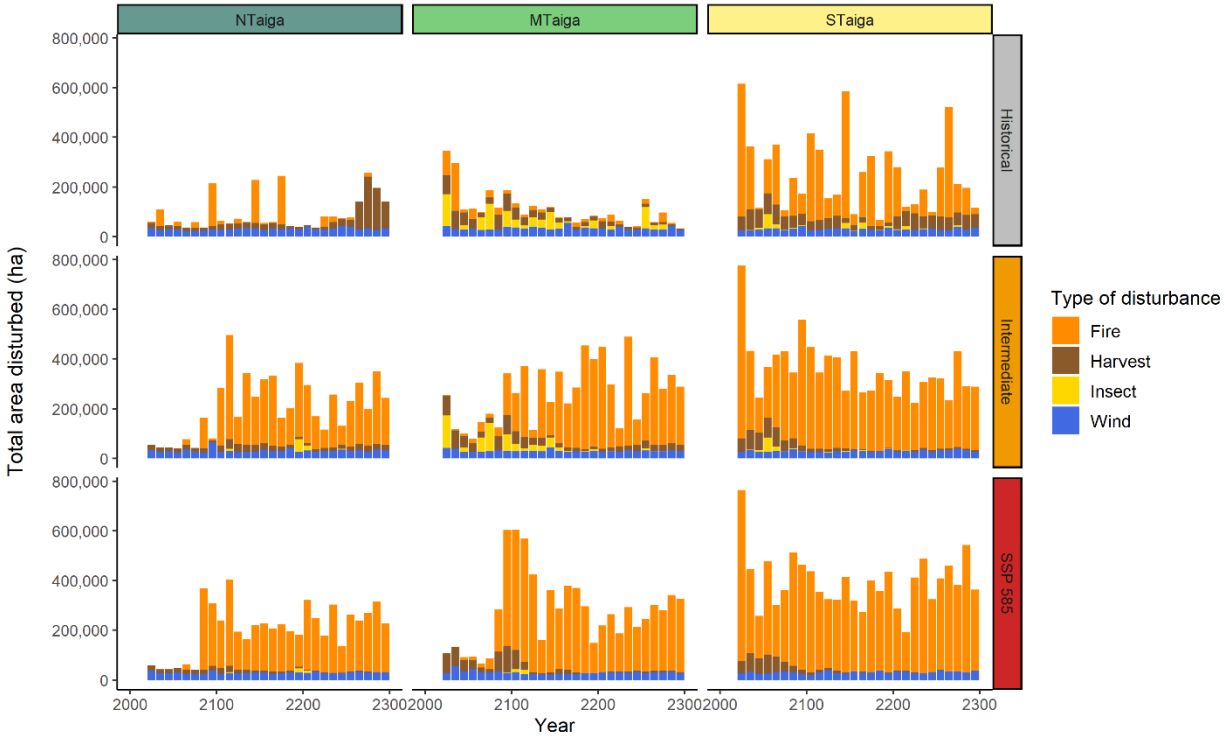
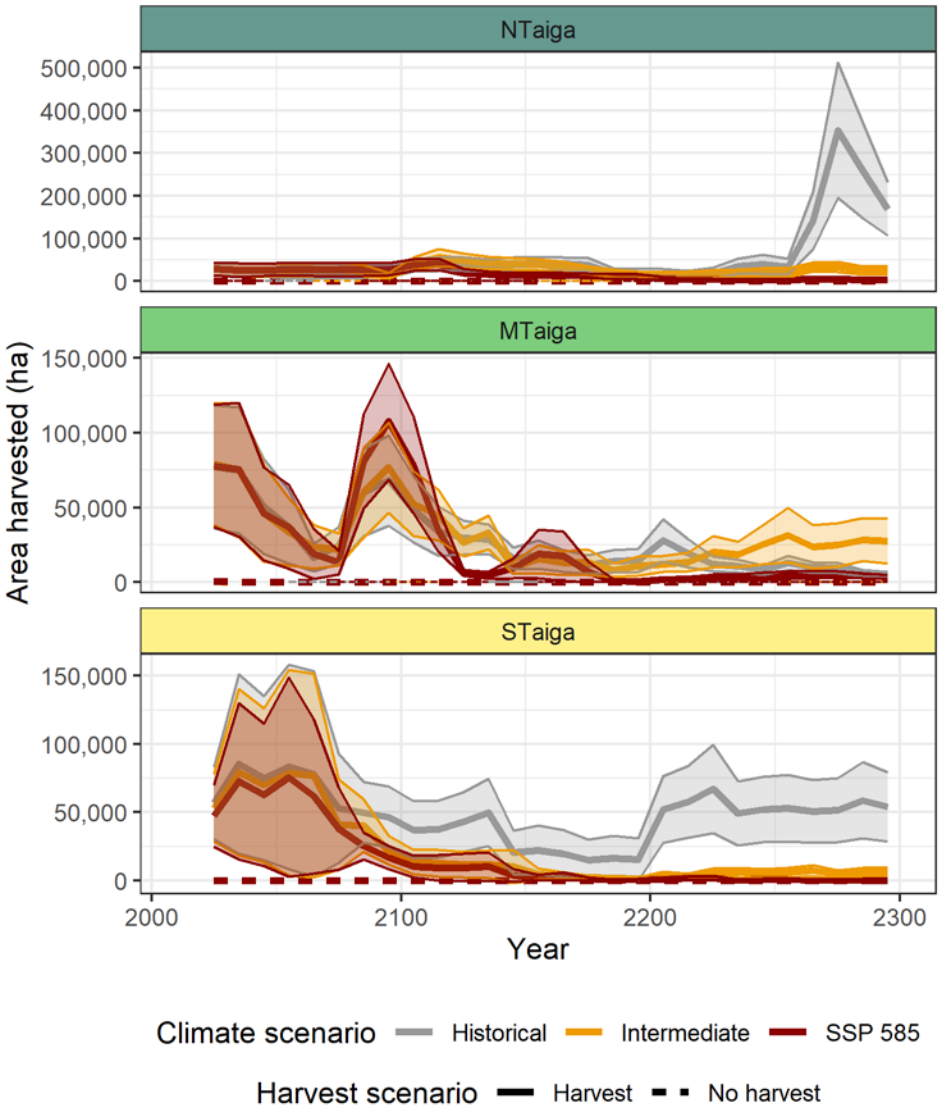


Fig. 2 Total area disturbed by disturbance type through time for each landscape and climate combination

In general, harvest rates generally decreased as latitude increased and as climate warmed (Fig. 3). Relatively short-term (decades) ups and downs in harvest rates were usually caused by demographic (age) availability; long term (century) shifts in harvest rates were caused by compositional availability (presence/absence of cohorts eligible for harvest) related to climate or disturbance effects on forest composition, age, and abundance. Notably, the spike in harvested area under historical climate in the NTaiga landscape resulted from the colonization of senescing shrub-dominated sites by trees and their maturation. In NTaiga and MTaiga, intermediate climate resulted in more (compared to Historical) area harvested (availability increased) until about 2200 and then area harvested dropped below Historical levels (availability decreased). In STaiga,

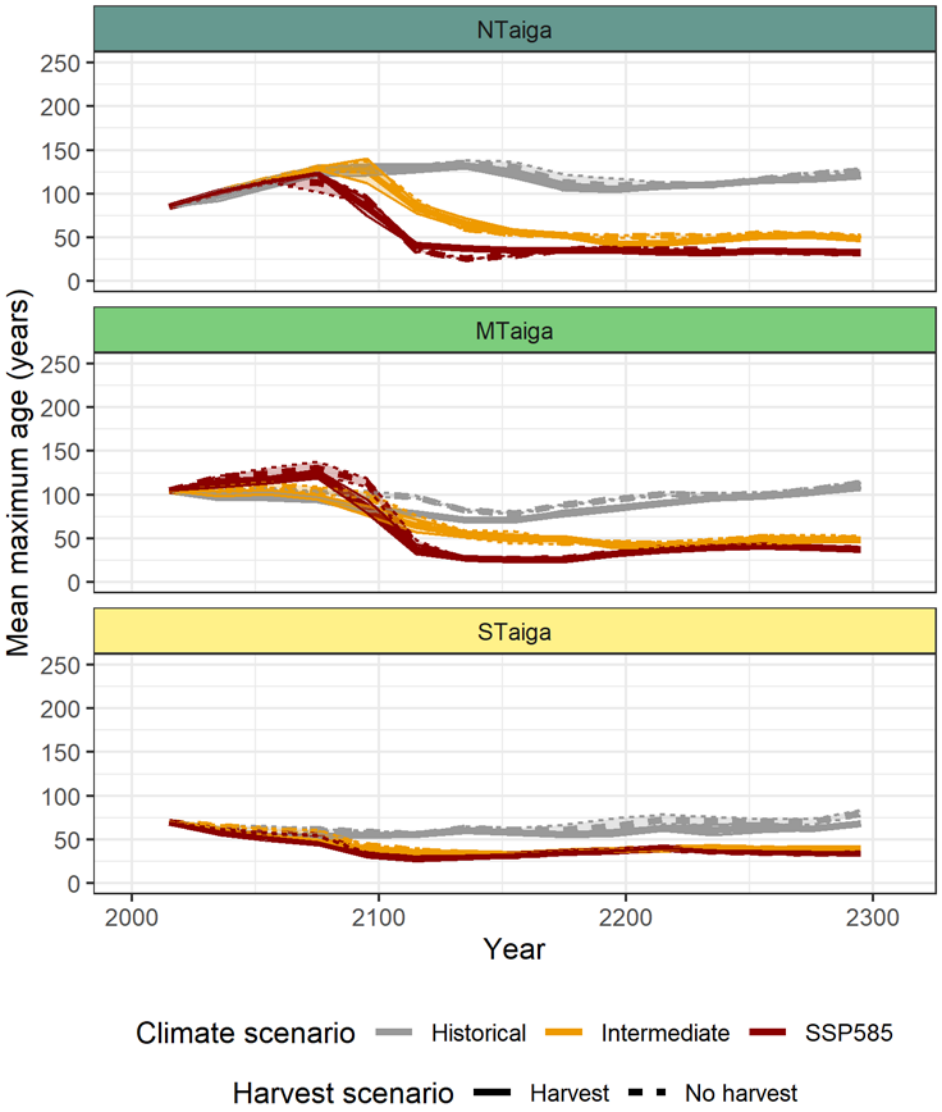
346 intermediate climate produced the same area harvested as SSP585 climate, which was
347 considerably lower than under Historical climate after 100 years. The SSP585 climate drove the
348 availability of eligible cohorts (for harvest) to very low levels by 2200 in all landscapes because
349 most cohorts were kept below minimum age constraints (Fig. 4, Table 3), driven by shortened
350 rotation intervals for disturbances. In terms of the amount of wood (total biomass) removed, the
351 general trends were very similar, but the biomass removed was much less as latitude increased
352 because of less productivity, longer harvest rotation lengths, and more unforested sites to the
353 north (Fig. S1, shown after Appendix).



354

355 **Fig. 3** Area harvested through time by Climate and Harvest scenario. Envelopes show one

356 standard deviation of four replicates. Note that y-axis scaling varies



357

358 **Fig. 4** Mean (across active cells) maximum cohort age by harvest activities through time by

359 Climate and Harvest scenario. Envelopes show one standard deviation of four replicates

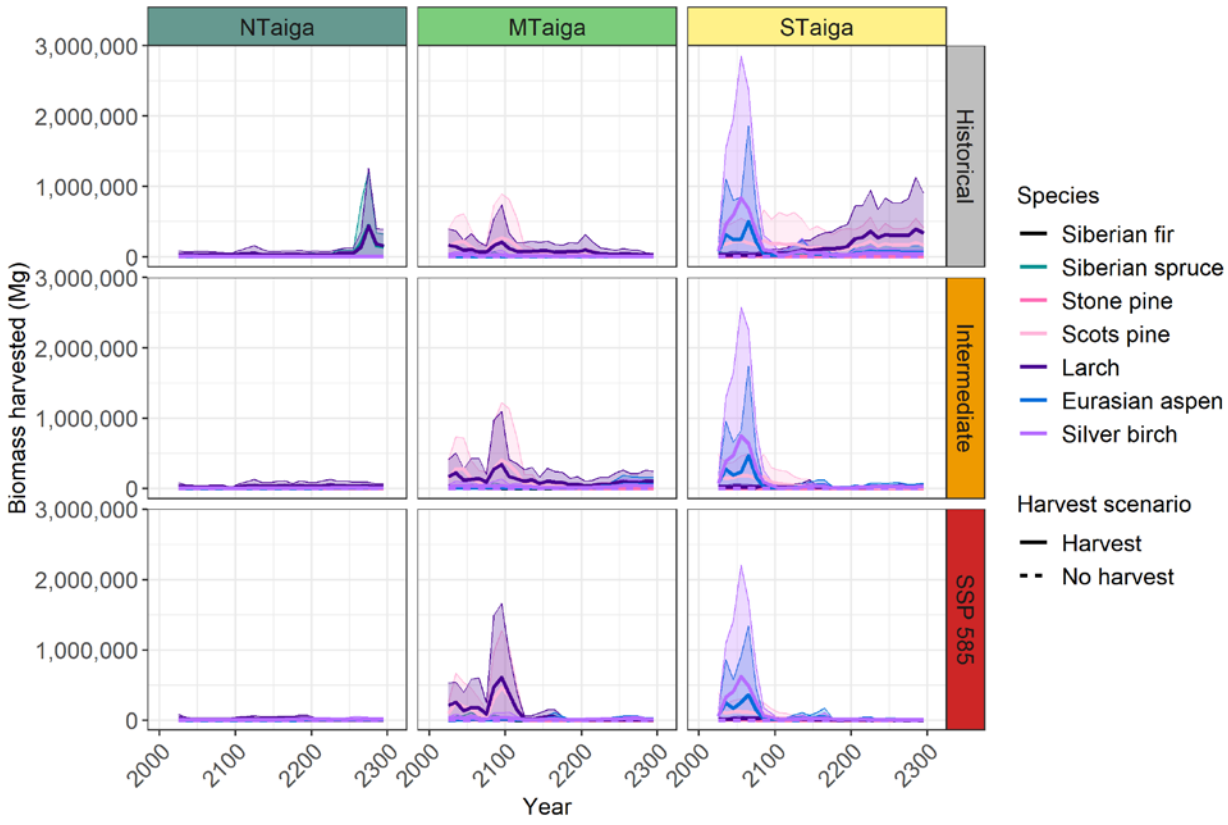
360

361 The species most likely to be harvested varied by latitude (Fig. 5) because availability varied

362 by latitude. Aspen and birch were initially very prevalent in the STaiga landscape (perhaps

363 inaccurately high in the initial conditions map) but were gradually replaced by larch and Scots

364 pine under Historical climate because fire intensity (as simulated by the model) lessened through
365 time. Mature trees (of all species) eventually became scarce under both climate change scenarios
366 on all landscapes because increased disturbance caused most cohorts to remain too young,
367 resulting in very low harvest rates. Aspen and birch modestly increased late in the simulations in
368 the southern two landscapes under climate change because of an increase of fire that favored
369 their regeneration.



370

371 **Fig. 5** Biomass (by species) removed by harvest through time by Climate and Harvest scenario.
372 Envelopes show one standard deviation of four replicates

373 **Forest composition**

374 Our simulations showed that two of the experimental factors (latitude and climate) produced
375 interacting effects on species abundance (Fig. 6), but the Harvest factor had little effect (not

shown). Latitude generally determined the species present and increasingly severe climate change increasingly caused a substantial change of winners and losers.

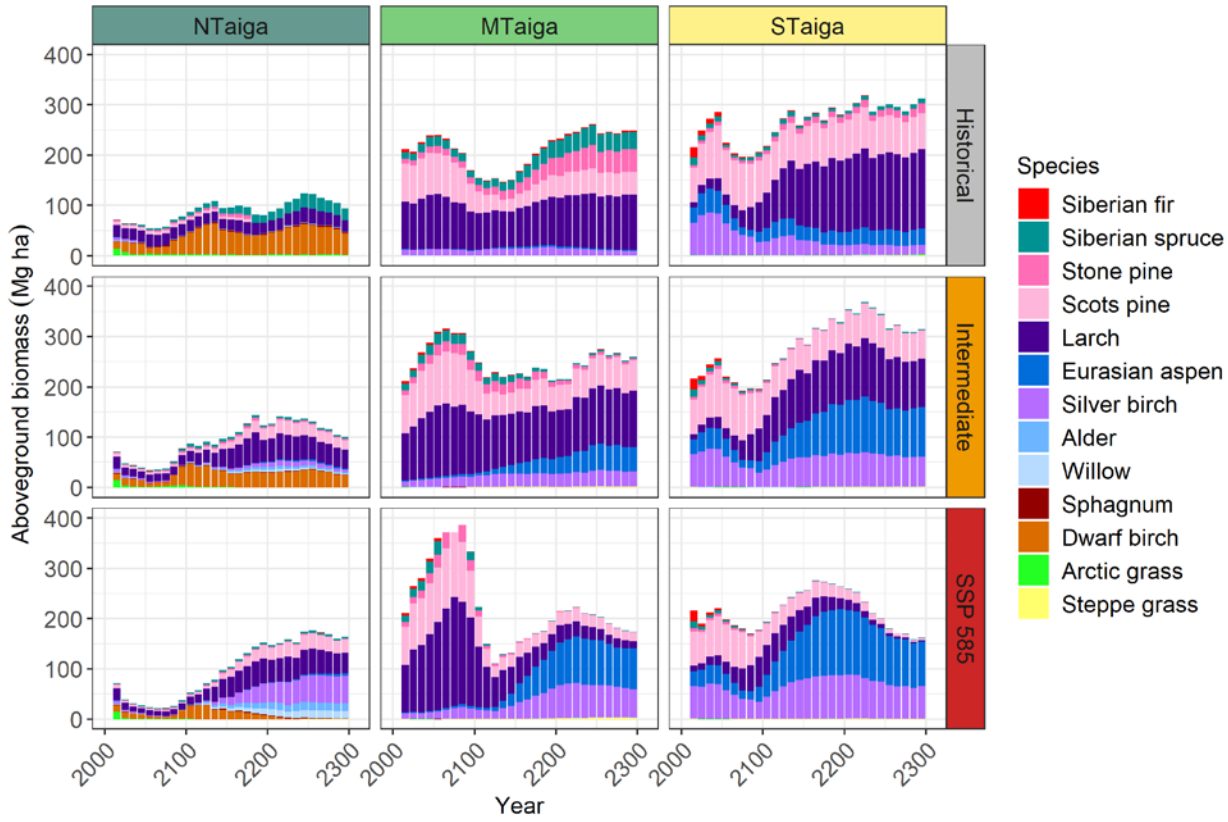
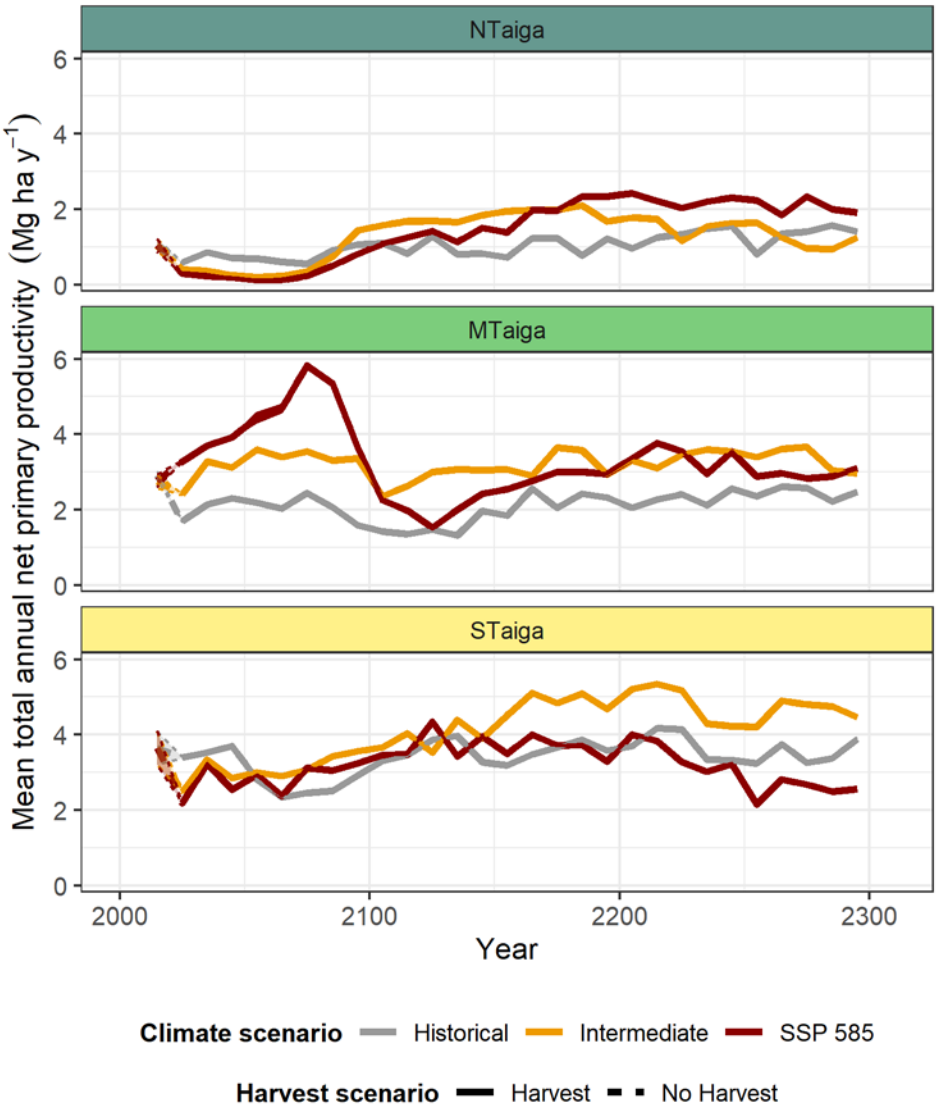


Fig. 6 Mean biomass density of each species through time across all active cells by Climate and just the All-Disturbances (including harvest) scenario. Bars are stacked in the order shown in the legend

Carbon dynamics

Forest productivity was quantified as the total (all simulated species) mean (all active landscape cells) annual net primary productivity. Productivity generally decreased with increasing latitude and increased with climate change, although in the southern two landscapes, the SSP585 climate resulted in declining productivity after 2200, especially in the STaiga (Fig. 7) mostly due to heat-related stress (in mid-summer) and increased disturbances. Harvesting did not noticeably alter

388 productivity (harvest/no harvest curves overlap), likely because harvesting affected a relatively
389 small proportion of the landscapes in each decade.

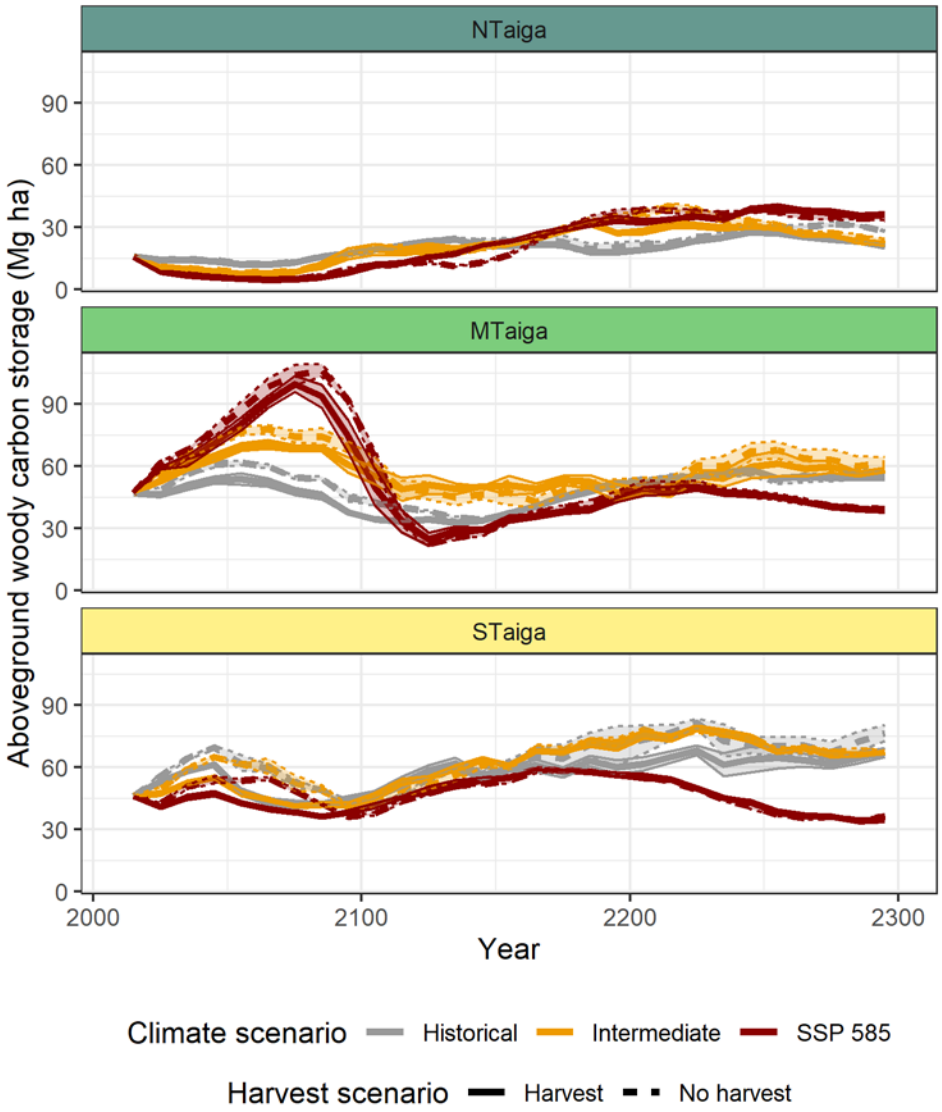


390

391 **Fig. 7** Mean total annual net primary productivity (annual sum of monthly net photosynthesis of
392 all species averaged across all active cells) through time by Climate and Harvest scenario.
393 Envelopes show one standard deviation of four replicates, and are generally less than line width

394

Carbon storage was quantified as mean aboveground live woody biomass (Fig. 8). Generally, carbon storage decreased with latitude and was slightly higher without harvest. In the MTaiga landscape there is a pronounced spike and decline of carbon in the first 100 years that is a consequence of initial condition demographics. In the first century, many younger cohorts of about the same age responded to an increasingly optimal climate (initially) to produce large amounts of live woody biomass (driven primarily by larch and Scots pine, Fig. S2). This was followed by a widespread demographic die-off of senescing cohorts (seen in all climates) and the subsequent slow (and sometimes incomplete) recovery reflects the effects of each climate on productivity in later years. In the northern landscape, the intermediate climate initially produced greater carbon storage, but ultimately the severe climate change scenario produced more by the end of the simulation period.



406

407 **Fig. 8** Mean (across all active cells) total aboveground live woody biomass (all species) through

408 time by Climate and Harvest scenario. Envelopes show one standard deviation of four replicates

409

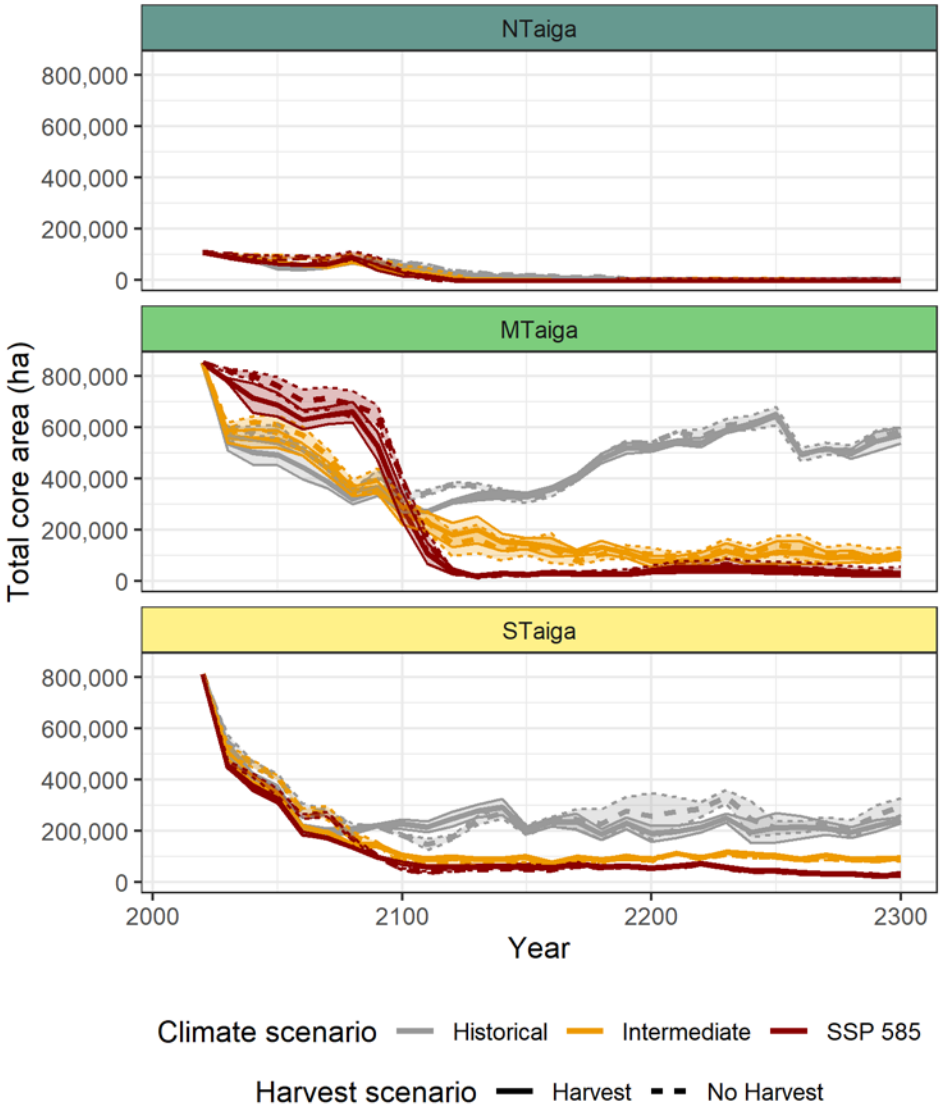
410 **Landscape fragmentation**

411 The area of core forest and the number of forest patches are indicators of fragmentation. The

412 NTaiga landscape was initially mostly open, with trees found primarily in riparian corridors, and

413 about 10% of that landscape consisted of core forest at the start of simulation, but core area

414 rapidly declined near the end of the 21st century (Fig. 9). In the southern two landscapes climate
415 change eventually reduced the area of core forest below Historical climate levels, while the no-
416 harvest treatment was less fragmenting, as expected. When core area approached zero, the
417 difference between the Harvest and No Harvest scenarios became negligible.
418



419

420 **Fig. 9** Mean total area of core habitat on each landscape by Climate and Harvest scenario. Core
421 habitat was defined as forested cells >300 m from an "Open" cell (defined in Table 5).

422 Envelopes show one standard deviation of four replicates. Decline in the first 10 years is an
423 artifact of initial conditions that inadequately represented prior disturbances
424
425 The northern landscape initially had fairly large contiguous patches of trees in riparian
426 corridors, but the invasion of trees into open areas generally resulted in large increases in forest
427 patch number because most invaded cells formed a new patch (Fig. 10). The southern two
428 landscapes had a matrix of forest initially, thus forming a low number of forest patches.
429 Harvesting generally increased the number of forest patches under all climate scenarios although
430 the difference was rarely significant (overlapping envelopes).
431

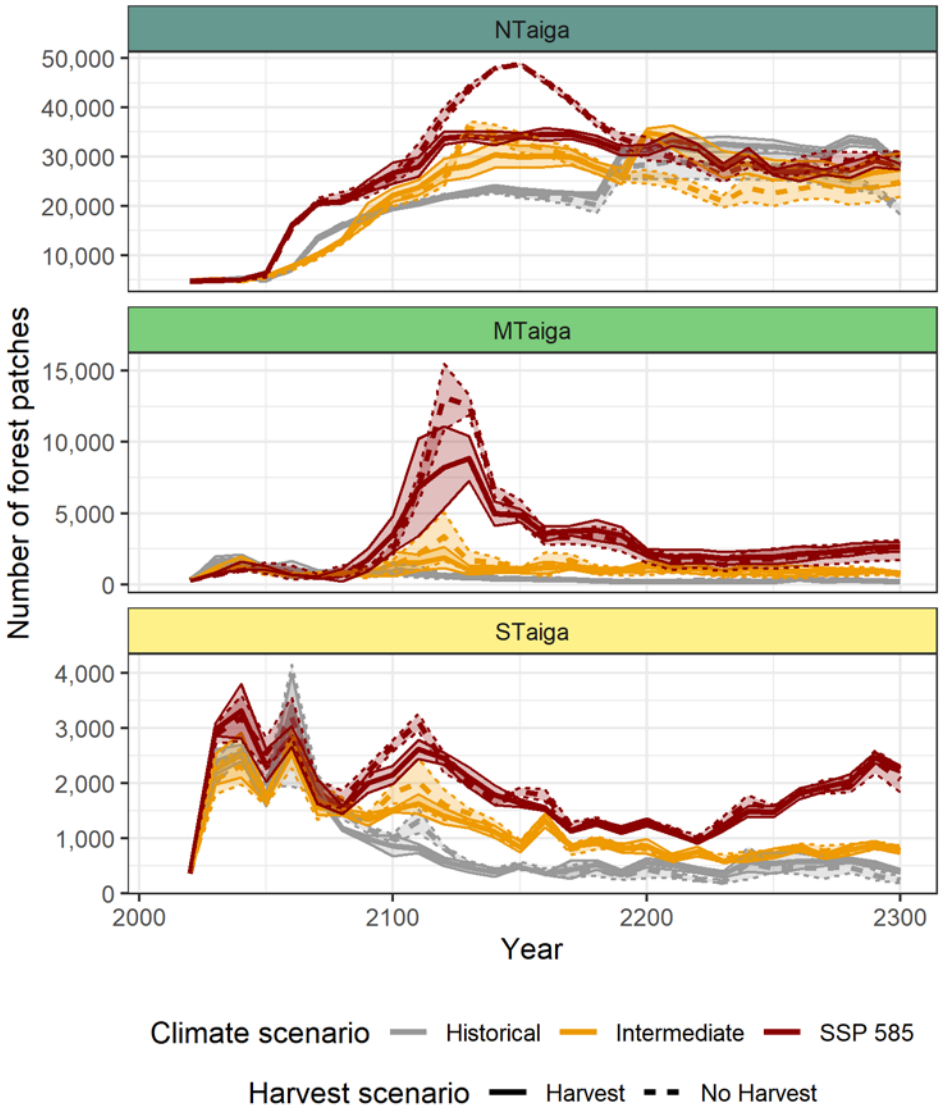


Fig. 10 Mean number of forest (Table 5) patches (rook's case) on each landscape by Climate and Harvest scenario. Envelopes show one standard deviation of four replicates. Note that y-axis scaling varies

Discussion

Our results showed several things quite clearly. 1) The current harvesting regime does not have much of an impact on Siberian ecosystem functions and landscape patterns compared to the

dominant effect of fire, and 2) *status quo* forest management strategies were sustainable until the end of the century (~2100), but will be unable to sustain most current forest ecosystem functions and services after 2150 under climate change, suggesting that adaptive management will be necessary. Specifically, climate change generally reduced the amount of timber available for harvest, and severe climate change nearly eliminated harvest activity by the year 2200 in all landscapes (Fig. 3, Fig. S1). Additionally, 3) productivity and carbon storage were generally increased by moderate climate change, but severe climate change tended to produce less of an increase in the southern landscapes. Harvesting had a minor effect on productivity and carbon storage primarily because current stand age constraints limited harvest rates. 4) Harvesting also had a minor effect on forest composition and age, while climate change produced a gradual shift in composition and an increase in the frequency of fire disturbance, which reduced the average age of the forest. 5) Multiple functions of all landscapes were generally reduced by climate change, and some functions were almost completely degraded. Declining harvest rates induced by climate effects on timber availability suggest that "climate-smart" management strategies (to produce future forests that sustain critical ecosystem goods and services, *sensu* Millar et al. 2007) are indicated and further research is needed to determine what an effective strategy might look like.

Our first hypothesis (H1) was that climate change would increase the amount of tree biomass as both stored carbon and wood available for harvest. We found that carbon storage was generally highest under Intermediate climate, but lowest under severe climate change (Fig. 8). There is evidence that plants will acclimate to elevated CO_2 such that extremely elevated CO_2 will not have an extreme fertilizing effect (Franks et al. 2013), while elevated temperatures will elevate heat stress and water demand (Allen et al. 2015). Our model includes these effects, and

463 our results show how they will play out over 280 years in these biomes. Harvest generally
464 reduced carbon storage, but the effect was quite small compared to climate effects and the
465 interacting factors simulated by the model. Climate change clearly altered the tree species in
466 which carbon was stored (Fig. S2). Current age constraints on harvest will almost certainly be
467 relaxed in the future in response to increasing tree productivity and shorter fire return intervals,
468 which should make current harvest rates more likely to be sustained, but also reducing carbon
469 storage even more than seen in our results. Taken together, this suggests that the carbon storage
470 function of these landscapes is at great risk from climate change. Our hypothesis (H1) was
471 supported for Intermediate climate change but not for severe climate change, and it was better
472 supported in terms of carbon storage than for wood harvested.

473 We hypothesized (H2) that total annual net primary productivity (forest productivity) will
474 increase because both climate change (CO_2 fertilization and lengthened growing seasons) and the
475 general reduction of forest age by harvesting will increase growth rates. Forest productivity was
476 very responsive to climate, with almost no response to harvest specifically (Fig. 7). The climate
477 effect likely also reflected an alteration of species composition apart from harvest activities (Fig.
478 5). Thus, our hypothesis (H2) was supported, but only for one of the reasons posited. As noted
479 earlier, the current harvest regime (specified in the Russian Forest Code) was quite generic and
480 rotation lengths did not vary through time in response to changing productivity. It is conceivable
481 that silvicultural treatments designed to maximize the productivity of specific stands would have
482 a more detectable effect. We did not simulate planting of better adapted species as part of the
483 harvest prescriptions (*sensu* Gustafson et al. 2023b), a practice that may have produced a greater
484 response to harvesting. Intermediate climate change usually produced the greatest productivity,

485 although the specific effect depended on the species found on (or invading) each landscape (see
486 Fig. S2).

487 Our third hypothesis (H3) stated that harvesting and climate change would interact to
488 increase the fragmentation of forests (less core habitat and higher edge density). We found that
489 harvesting increased the fragmentation of core habitat (as expected), although climate change
490 decreased core habitat to such an extent by the year 2100 (likely through increased fire) that the
491 effect of harvest was not detectable (Fig. 9). Climate change did not increase the fragmenting
492 effect of harvesting as we expected from our hypothesis, and in fact the harvest fragmenting
493 effect essentially disappeared after 200 years of climate change.

494 Our simulation of timber harvest allowed harvest rates to respond to timber availability after
495 the first rotation (Table 3), although the rotation lengths (minimum age constraints) did not
496 change. Climate change generally reduced the amount of timber available for harvest, and severe
497 climate change almost nearly eliminated harvest activity by the year 2200 in all landscapes (Fig.
498 3, Fig. S1), mostly caused by fires that kept the forests quite young. Intermediate climate change
499 increased the biomass (proxy for volume) removed by harvest of some species on some
500 landscapes (Fig. 5), but severe climate change reduced harvesting of all species.

501 The LANDIS-II Harvest extension is not able to control harvest levels by available volume
502 or biomass, only by area harvested and/or age. We simulated harvest using generic silvicultural
503 prescriptions that reflect current harvest rotation lengths (minimum age for harvest) on each
504 landscape. Because the minimum age parameters became very constraining as disturbance
505 intervals shortened, the amount of harvest was not sustained. However, it is almost certain that
506 real forest managers will find ways (i.e., adaptive management) to harvest some of the biomass
507 that is present on all landscapes in all decades (Fig. 8). For example, the increased productivity

under climate change (especially moderate climate change) that our simulations revealed in some or all study landscapes should reduce the time required for timber species to reach merchantable sizes, thereby allowing managers to reduce rotation lengths to reduce exposure to disturbances.

Other adaptations might include assisted migration of tree species expected to thrive under the conditions of the future, or hastening conversion to other endemic types (e.g., hardwoods). Our results show some clear shifts of forest types, especially under extreme climate change. Climate smart management might embrace these shifts along with the productivity gains associated with CO_2 fertilization and longer growing season, allowing shorter rotations. This will likely have socio-economic implications in terms of wood processing infrastructure and the markets for the forest products that can be produced.

Our study is novel in that it was conducted using a landscape-scale model featuring process-based simulations of seed dispersal, establishment, growth and competition (both responding to abiotic drivers including permafrost thawing) combined with spatially explicit simulation of several major disturbances. Our approach allowed current harvest regimes to respond to the dynamic forest composition produced by the other simulated processes, so that all response variables represent emergent properties of the interacting drivers of the ecosystem. Our study is also one of a just a few to attempt to assess climate impacts on forest resources in high latitude ecosystems. Other studies were conducted using panels of experts (Jansson et al. 2015) or were aspirational in nature (Bastian et al. 2015; Bukvareva et al. 2015), so our study provides a process-based complement to those studies.

Caveats

It is important to note a few caveats related to our methods. First, we did not simulate the building of access roads (or processing mills) that facilitate the harvest of trees. We assumed that

531 if timber is there, infrastructure will be built to extract it. Second, we did not simulate any tree
532 planting activities, including assisted migration, because that is not part of current practice in
533 these landscapes. Third, we did not simulate any land use change, such as land clearing for
534 settlements or other permanent uses such as roads and natural resource extraction. Fourth, we did
535 not include stochasticity in climate, initial landscape conditions, or species and abiotic model
536 parameters. Thus, our variability envelopes reflect only the variability in the stochastic processes
537 simulated within the model (e.g., disturbances, cohort establishment, some site-level growth and
538 competition processes). Finally, our forest productivity estimates include non-commercial
539 species (shrubs, grasses), and therefore reflect the general effect of the treatments on plant
540 productivity.

541 **Future research**

542 Our study suggests interesting options for future research. We did not simulate any "climate-
543 smart" forest management practices (such as adapting to altered forest composition and growth
544 rates, assisted migration strategies, or adopting new indicators of ecosystem sustainability) that
545 will almost certainly be needed in the future to maintain ecosystem functions and services in
546 arctic and boreal ecosystems. The primary reason we did not simulate any generic climate-smart
547 forest management scenarios is that we found no proposed options for Siberia (neither adaptive
548 or transition strategies) published in the literature. The standard climate-smart strategies of
549 planting more southerly tree species are a challenge in Siberia because areas to the south of
550 Russia are often shrub and not tree-dominated. Conceptual research is needed to develop some
551 climate-smart strategies for Siberia and then some applied research to assess the efficacy of such
552 strategies in the boreal forests of Eurasia. Our modeling approach shows promise for
553 investigating one facet of such an assessment by including many interacting drivers of forest

554 dynamics at landscape scale, such as seed dispersal, disturbance and climate (e.g., Gustafson et
555 al. 2023b). Research into the ability of adaptive forest management to respond to altered
556 disturbance regimes and mitigate the negative consequences of climate change for forests and
557 forest products is also needed. Another potential avenue for future research is to use LANDIS
558 outputs to estimate habitat quality for representative animal species under alternative climate and
559 management futures (e.g., Lucash et al. 2022).

560 Conclusions

561 We were able to draw three main conclusions from our study. 1) Climate change has the
562 potential to greatly alter ecosystem functioning in the vast boreal forests of Eurasia, especially in
563 the far north. Some impacts are positive (productivity), especially under Intermediate climate
564 change, but some are negative (increasing mortality from natural disturbances, fragmentation),
565 especially under severe climate change. 2) Harvesting as a specific driver of change in these
566 boreal forests is likely to be relatively minor except as a forest fragmentation process. All
567 disturbances combined had a much greater effect (Gustafson et al. in review) on ecosystem
568 processes. 3) Our results provide compelling evidence that *status quo* forest management is not
569 sustainable in these ecosystems beyond this century, but they do highlight the potential for
570 adaptive management, facilitated by increasing productivity and improved conditions for certain
571 species. Although our study did not investigate what management strategies might be necessary
572 to generate sustainable ecosystem functions and services, our modeling approach is well-suited
573 for such studies.

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3. **Appendix.** Siberian silk moth (*Dendrolimus siberica* Chetverikov) disturbance regime parameterization.

Siberian silk moth is a native species of Siberia that is expanding its range both west (Gninenko & Orlinskii 2002) and north (Kharuk et al. 2018), with records of disturbance at the longitude of our Siberia study region since the turn of the 20th century (Pavlov et al., 2018). While its outbreaks are often described in the literature as periodic (Kharuk et al., 2003; Kondakov, 1974), widespread impacts appear episodic in nature (Pavlov et al. 2018), with outbreaks expanding in elevation and latitude with recent climate warming and thought to be triggered by drought (Kharuk et al. 2018). The insect has a complex life cycle with a larval stage that typically spans two years, where instars emerging in spring focus on new foliage, then expand to all age classes of conifer needles (Kirichenko & Baranchikov 2007). Outbreaks first appear as epicenters (hot spots) that typically start in environmentally favorable (warm, dry) sites in areas with high concentration of its primary host (Kondakov 1974; Sultson et al. 2021). Its rank order of host preference is larch > fir > 5-needle pine > spruce > 2 needle pine (Kirichenko and Baranchikov 2007). However, larch as a deciduous conifer is generally more resilient to defoliation (Leontiev 2015). The outbreak spreads over time to create large patches of impacted forests (Sultson et al. 2021). Mortality in impacted areas is typically exacerbated by stem-feeding insects (i.e., beetles; Kharuk et al. 2016; Zhirin et al. 2016) and also fire (Kharuk & Antamoshkina 2017). The disturbance regime was implemented using the Biological Disturbance Agent Extension of LANDIS-II (Sturtevant et al. 2024) to mimic these characteristics.

Tree species susceptibility (i.e., the probability of attack) was parameterized using the "appropriateness index" of Kirichenko and Baranchikov (2007), rescaled to range between the

most palatable host (*Larix siberica*; 1) and the least palatable host (*Pinus sylvestris*, 0.1) (Table A1). Our assumptions underlying parameters for vulnerability (likelihood of dying from an attack) were: 1. Once defoliation occurs, all age classes are vulnerable, 2. Deciduous conifers (i.e., *Larix siberica*) are more resilient to defoliation, 3. The vulnerability of fir and spruce are enhanced by secondary bark beetle impacts above a certain size threshold, using age as a proxy. 4. *Pinus sylvestris* mortality is primarily spill-over from other host species (Table A1).

Table A1. Host tree species susceptibility and vulnerability (see text for rationale).

	Susceptibility			Vulnerability	
Tree Species	Class 1 Age (value)	Class 2 Age (value)	Class 3 Age (value)	Baseline Age (value)	Beetle-enhanced Age (value)
Larix siberica	20-39 (0.25)	40-79 (0.50)	80+ (1.0)	All ages (0.35)	NA
Abies siberica	20-39 (0.21)	40-79 (0.42)	80+ (0.85)	0-39 (0.7)	40+ (1.0)
Pinus siberica	20-39 (0.20)	40-79 (0.40)	80+ (0.80)	All ages (0.7)	NA
Picea obovata	20-39 (0.12)	40-79 (0.25)	80+ (0.50)	0-39 (0.7)	40+ (0.85)
Pinus sylvestris	20-39 (0.02)	40-79 (0.05)	80+ (0.10)	All ages (0.25)	NA

Temporal occurrence of outbreaks restricted to years when 1. cumulative active temperatures (> 10 ℃) were between 1200 ℃ and 2200 ℃ (Kharuk et al. 2017), 2. when mean August temperature was > 13.5 ℃ (Dergunov & Yakubailik 2019), and 3. during drought conditions defined by the Standardized Precipitation-Evapotranspiration Index (SPEI; https://spei.csic.es/) (Kharuk et al. 2017). For SPEI , we evaluated different combinations of summer months, temporal averaging across years, and thresholds in the index that best matched the spatial locations and temporal occurrences of outbreaks documented by Pavlov et al. (2018). Most plausible drought triggers were 2-year average SPEI for summer months (June-August) with a -0.5 requirement for new epicenters, and less extreme drought (-0.2) allowing existing outbreaks to continue spreading. Outbreak epicenters required high host concentrations (i.e., >= 0.7 average susceptibility) to initiate, and could spread up to 1500m annually, just beyond the

high end of empirically estimated dispersal distances (Kharuk et al. 2016). New epicenter numbers in each climatically defined outbreak time step was defined by a Michalis-Menton function of the proportion of eligible to total sites, with Nmax = 250 and Km = 0.1.

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4. **SUPPLEMENT FIGURES** – included here for review purposes.

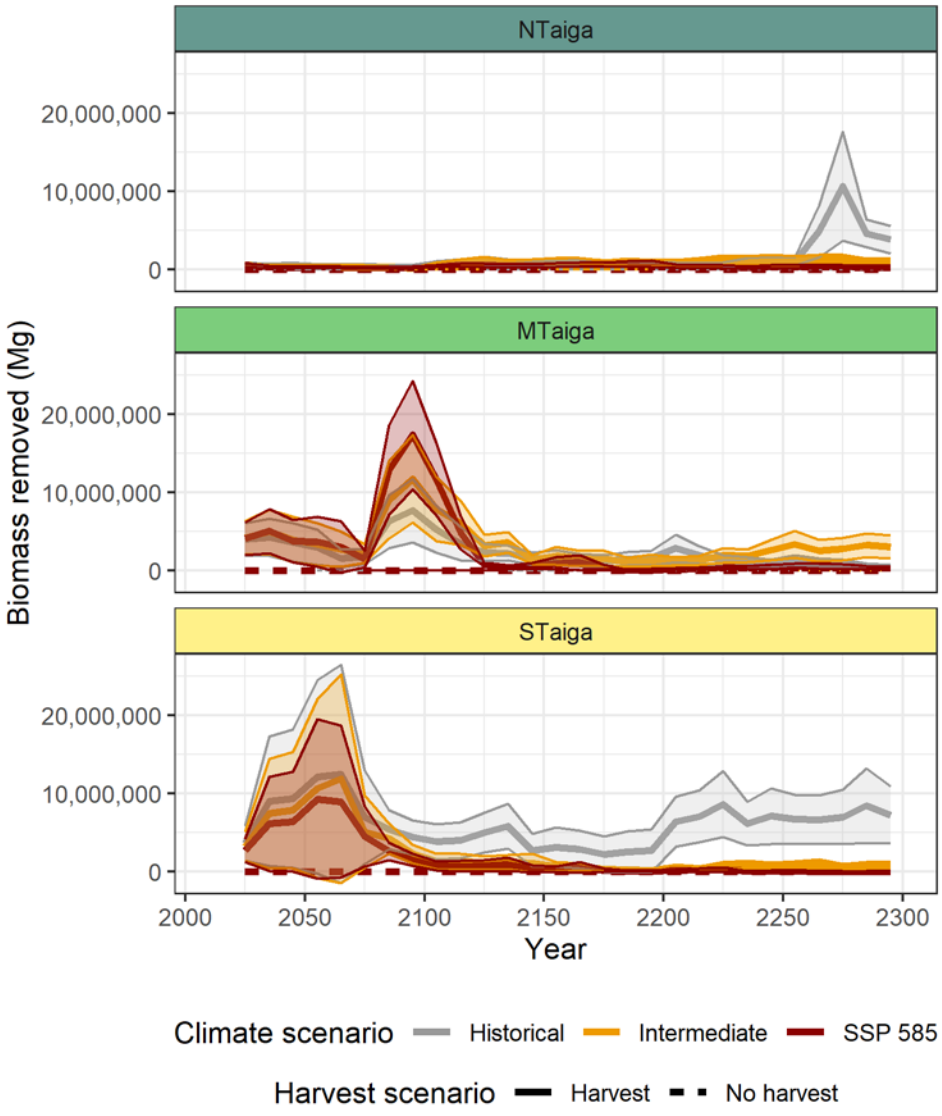
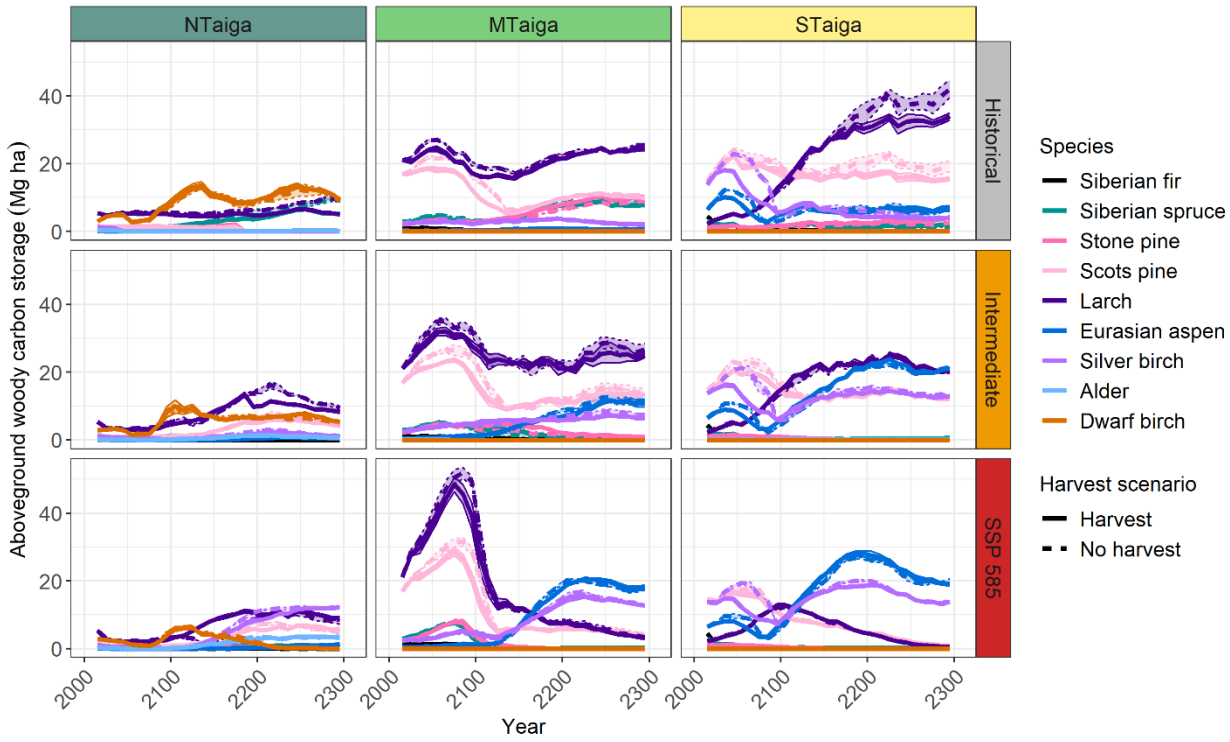


Fig. S1 Total woody biomass removed by harvesting through time by Climate and Harvest scenario. Envelopes show one standard deviation of four replicates. See text for explanation of spike in the southern landscapes



896

897 **Fig. S2** Mean carbon storage by species by Climate and Harvest scenario. Envelopes show one

898 standard deviation of four replicates

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