

Article

Seed Harvesting and Climate Change Interact to Affect the Natural Regeneration of *Pinus koraiensis*

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Abstract: The poor natural regeneration of *Pinus koraiensis* is a key limitation for restoring the primary mixed *Pinus koraiensis* forests. Seed harvesting and climate change are the important factors that influence the natural regeneration of *Pinus koraiensis*; however, it is hard to illustrate how, in synergy, they affect its regeneration at the landscape scale. In this study, we coupled an ecosystem process model, LINKAGES, with a forest landscape model, LANDIS PRO, to evaluate how seed harvesting and climate change influenced the natural regeneration of *Pinus koraiensis* over large temporal and spatial scales. Our results showed that seed harvesting decreased the abundance of *Pinus koraiensis* juveniles by 1, 14, and 18 stems/ha under the historical climate, and reduced by 1, 17, and 24 stems/ha under the future climate in the short- (years 0–50), medium- (years 60–100), and long-term (years 110–150), respectively. This indicated that seed harvesting intensified the poor regeneration of *Pinus koraiensis*, irrespective of climate change. Our results suggested that seed harvesting diminished the generation capacity of *Pinus koraiensis* over the simulation period. Seed harvesting reduced the abundance of *Pinus koraiensis* at the leading edge and slowed down its shift into high-latitude regions to adapt to climate change. Our results showed that the effect magnitudes of seed harvesting, climate change, their interaction and combination at the short-, medium- and long-term were –61.1%, –78.4%, and –85.7%; 16.5%, 20.9%, and 38.2%; –10.1%, –16.2% and –32.0%; and –54.7%, –73.8%, and –79.5%, respectively. Seed harvesting was a predominant factor throughout the simulation; climate change failed to offset the negative effect of seed harvesting, but the interactive effect between seed harvesting and climate change almost overrode the positive effect of climate change. Seed harvesting, climate change, and their interaction jointly reduced the natural regeneration of *Pinus koraiensis*. We suggest reducing the intensity of seed harvesting and increasing silvicultural treatments, such as thinning and artificial plantation, to protect and restore the primary mixed *Pinus koraiensis* forests.

Keywords: seed harvesting; climate change; interactive effect; regeneration; *Pinus koraiensis*



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1. Introduction

Pinus koraiensis is a climax species in the temperate forests of Northeast China [1,2]. It has high ecological and economic values, including carbon sequestration, timber, and seed products [3]. Due to excessive timber harvesting in the past fifty years, the dominance of *Pinus koraiensis* has evidently decreased, and the primary mixed *Pinus koraiensis* forests have degraded into secondary forests [4,5]. The Chinese government implemented the Natural Forest Conservation Project in 1998 and the Commercial Harvesting Exclusion Policy in 2014 to restore the primary forests and increase forest stocks [6,7]; however, these projects and policies remarkably reduced local incomes from timber. *Pinus koraiensis* seeds are large and edible, with a high content of pinolenic acid, and thus they have various health effects; this determines their high economic value [8]. Given the economic value of

Pinus koraiensis seeds, predatory seed harvesting gradually became an important income source for the local population [9]; however, this harvesting might further aggravate the poor natural regeneration of *Pinus koraiensis*. Previous studies showed that predatory seed harvesting significantly decreased seed provenance and would reduce the dominance of *Pinus koraiensis* in the long term [10]; this would hinder the restoration of the primary mixed *Pinus koraiensis* forests under future climate change scenarios.

The temperate forests in Northeast China are being affected by climate change. Predictions based on both the General Circulation Models (GCMs) and the regional Climate-Weather Research and Forecasting model (CWRF) indicated that Northeast China would have a warm and wet climate in the future, especially in summer and that precipitation would significantly increase [11,12]. The warming climate has caused tree species to migrate towards regions with a higher latitude and elevation in order to adapt to climate change [13]. A recent dendrochronological study showed that the growth of *Pinus koraiensis* at the trailing edge and in the young age cohort was limited by the warm and dry climate conditions [14], which might have adverse effects on its migration. Another study showed that *Pinus koraiensis* would shift to higher latitude regions as a result of a warm and wet climate [11]. However, seed harvesting reduces the provenance of *Pinus koraiensis* and the probability of its regeneration, which may be unfavorable for its migration into suitable regions. Given the uncertainties of climate and the negative effect of seed harvesting, it is essential to clarify how seed harvesting and climate change impact on its migration for the successful adaptation of *Pinus koraiensis* to the future climate.

Climate change generally interacts with disturbances to impact forest landscapes [15]. A previous study found that climate change and tree harvesting had interactive effects on species distribution and that the interaction between these factors accelerated the contraction or expansion of distributions induced by climate change [16]. *Pinus koraiensis* and its associated species are both symbiotic and competitive; climate change and seed harvesting can alter these interspecific relationships. Climate change altered forest composition by promoting species that were adaptive to future climate while suppressing maladaptive species [11]. Seed harvesting directly reduced the quantity of potential germination seed, thereby potentially decreasing the regeneration of *Pinus koraiensis* and indirectly promoting the recruitment of species with a similar ecological niche. [10]. Whether there is an interaction between climate change and seed harvesting is unknown.

It is challenging to assess the effects of seed harvesting and climate change on the natural regeneration of *Pinus koraiensis* at the landscape scale. Seed harvesting, a landscape process, synergizes with competition at the stand scale, seed dispersal at the landscape scale, and climate change at the regional scale to affect *Pinus koraiensis* regeneration. Most previous studies investigated and monitored the adverse effects of seed harvesting on *Pinus koraiensis* seed or seedling banks at the plot or stand scale [4,9,17,18]. Still, it is hard to interpret how seed harvesting functioned over larger temporal and spatial scales, in particular under climate change scenarios. A forest landscape model can simulate the synergistic effects of population dynamics, seed dispersal, and harvesting on forests at large temporal and spatial scales. In addition, it can be coupled with an ecosystem process model to incorporate the effect of climate change [19,20]. Thus, coupling a forest landscape model with an ecosystem process model provides a feasible tool for evaluating the effects of seed harvesting and climate change on the natural regeneration of *Pinus koraiensis* at the landscape scale.

In this study, we evaluated how seed harvesting and climate change impact the natural regeneration of *Pinus koraiensis* at the landscape scale using a forest landscape model, LANDIS PRO, in the Xiaoxing'an Mountain, Northeast China. Specifically, we aimed to address (1) how the natural regeneration of *Pinus koraiensis* varies under alternative scenarios of seed harvesting and change climate combination; (2) whether seed harvesting reduces the regeneration capacity of *Pinus koraiensis* at the landscape scale and slows down its migration into high-latitude regions regardless of climate scenarios; and (3) whether there is an interactive effect between seed harvesting and climate change on the natural

regeneration of *Pinus koraiensis*. Additionally, if it exists, we investigated the magnitudes of the relative contribution of seed harvesting, climate change, and their interaction and combination in the short- (years 0–50), medium- (years 60–100), and long-term (years 100–150), respectively.

2. Materials and Methods

2.1. Study Area

We chose the Xiaoxing'an Mountains as the study area, which cover 1.5 million hectares, with longitude and latitude ranges of 127°50' E to 130°10' E and 47°05' N to 49°10' N, and with elevations ranging from 139 to 1429 m (Figure 1). The study area belongs to a temperate continental monsoon climate with a mean annual temperature from 1.0 to −1.0 °C and precipitation of 700 to 550 mm from the south to the north, respectively. The dominant soil is *Haplic Luvisols*, and distributes widely throughout the region. The study area is located in the transitional zone between a temperate forest and boreal forest, and the leading edges of some species are in this region, such as *Pinus koraiensis*. The typical primary mixed *Pinus koraiensis* forests include *Quercus mongolica* and *Pinus koraiensis* forests, *Picea koraiensis* and *Picea jezoensis*, *Abies nephrolepis*, and *Pinus koraiensis* forests, *Tilia amurensis* and *Pinus koraiensis* forests, *Betula costata*, and *Pinus koraiensis* forests. However, these primary forests have degraded into secondary forests because of the historical excessive timber harvesting. Forests in this region have been divided into three types for classified management: the special ecological welfare forests, the general ecological welfare forests, and the commercial forests to restore forest resources and increase stocks since the Natural Forest Conservation Project in 1998. Timber harvest was conducted to increase incomes for the locals in the general ecological welfare forests and the commercial forests but was excluded in the special ecological welfare forests before the year 2014. All commercial timber harvesting has been prohibited since the Commercial Harvest Exclusion Policy since the year 2014, and now seed harvesting is an important anthropogenic disturbance.

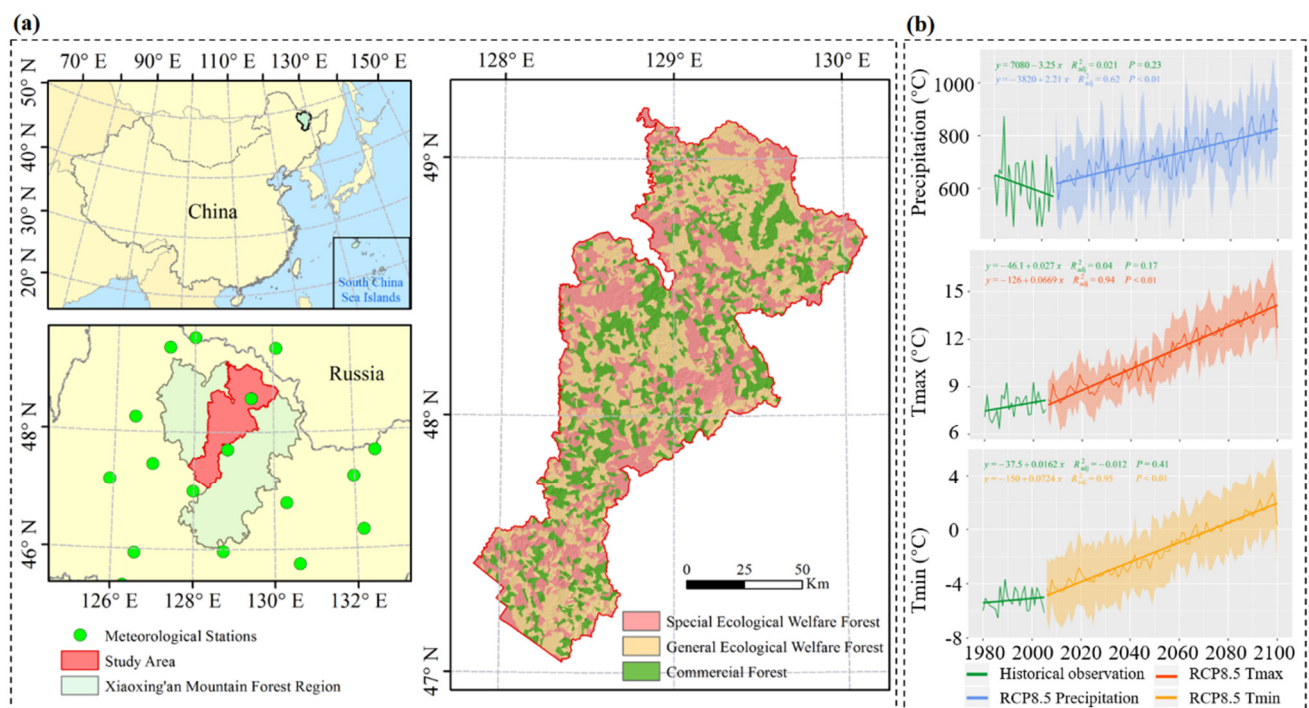


Figure 1. Geographical location and three categories of management zones of the study area (a), and the historical climate observation and future climates projected by the four General Circulation Models (GCMs) under the RCP8.5 scenario (b).

2.2. Climate Data

We obtained the maximum temperature, minimum temperature, precipitation, average wind speed, and average daily radiation from the China Meteorological Data Network from 1980 to 2009 as a baseline climate (<http://data.cma.cn/>, accessed on 24 February 2017). We selected the abovementioned climate variables under the representative concentration pathway 8.5 (RCP8.5) scenario predicted by the four GCMs from the Coupled Model Intercomparison Project phase 5 (CMIP5) as the climate change scenario (<https://esgf-node.llnl.gov/search/cmip5/>, accessed on 22 April 2016), since the RCP8.5 scenario with the highest emission provided the upper limit of climate change. The four selected GCMs included the Climate Model version 3 of the Geophysical Fluid Dynamics Laboratory (GFDL-CM3), the Hadley Center Global Environment Model version 2 Earth System (HadGEM2-ES), the Model for Interdisciplinary Research on Climate version 5 (MIROC5), and the Meteorological Research Institute Climate General Circulation Model version 3 (MRI-CGCM3). We chose the four GCMs since the temperature and precipitation predicted by them had large seasonal and annual differences which captured the uncertainties of future climate and they all output the climate variables used in our study [11].

2.3. LINKAGES 3.0 Model and Parameterization

LINKAGES, an ecosystem process model, incorporates succession and soil nutrient cycles to simulate forest dynamics at the stand scale with a one-year time step [21]. Individual regeneration is controlled by the growing degree per day, light, and water availability. Tree species growth and biomass accumulation are jointly regulated by growing degree per day, light and water availability, and soil available nitrogen. Mortality was determined probabilistically by annual tree growth of $\leq 10\%$ of maximum possible diameter growth and by a background rate threshold defined as $4.605/\text{maximum longevity}$ against which a random number was compared. Random draws less than or equal to the threshold lead to mortality. LINKAGES principally requires the inputs of species' biological traits, daily climate data, and soil data. Since LINKAGES needs daily climate data, it can capture the effect of subtle changes in climate on forest dynamics. The outputs of LINKAGES mainly comprise species area and biomass, soil nitrogen availability, soil organic matter, and net primary productivity.

We derived fifteen major species' biological traits, mainly included in Table 1, from the Flora of China (<http://frps.iplant.cn/>, accessed on 4 October 2018) and the previous studies in this region [11]. We interpolated the above climate elements under historical and future scenarios into different sites using R package “*meteoland*” [22]. We obtained soil data from the Soil Database of China for Land Surface Modeling (<http://globalchange.bnu.edu.cn/research/soil2.jsp>, accessed on 4 November 2018). We calculated each soil layer's field capacity and wilting point with the Century Model soil calculator (<https://www.nrel.colostate.edu/projects/century/soilCalculator.html>, accessed on 10 November 2018).

We used species biomass and total biomass under historical and future climate conditions to evaluate the species establishment probability (SEP) and the maximum growing space occupied (MGSO) in different land types, respectively, which were two critical parameters for LANDIS. We divided forest landscapes into eight land types with relatively homogeneous interiors and heterogeneous exteriors based on elevation, aspect, and the $\geq 10^\circ\text{C}$ cumulative temperature line. We assumed the SEP and MGSO were homogeneous in one land type but heterogeneous among land types. We ran LINKAGES with each species from a bare plot until the year 30 for 20 replicates under alternative climate scenarios and calculated the ratio of individual species biomass and the sum of all species biomass as the SEP. We executed LINKAGES with all species from the bare plot until the year 100 for 20 replicates under alternative climate scenarios and estimated the maximum total biomass reaching on each land type among climate scenarios as the MGSO [16].

Table 1. The major species parameters in the LINKAGES 3.0 model.

Species	DMX	DMN	B3	B2	G	D3	FT	TL
<i>Pinus koraiensis</i> Sieb. & Zucc.	2500	900	0.29	62.96	104.53	0.28	−35	12
<i>Picea jezoensis</i> var. <i>microsperma</i> (Lindl.) W.C.Cheng & L.K.Fu and <i>Picea koraiensis</i> Nakai	2500	600	0.35	63.62	87.79	0.19	−34	11
<i>Abies nephrolepis</i> (Trautv.) Maxim.	1800	400	0.40	67.36	87.65	0.23	−34	10
<i>Larix gmelinii</i> (Rupr.) Kuzen.	1900	400	0.32	60.27	87.92	0.42	−38	12
<i>Fraxinus mandshurica</i> Rupr.	2800	1000	0.34	67.26	121.90	0.19	−31	2
<i>Juglans mandshurica</i> Maxim.	2650	850	0.23	41.40	72.89	0.28	−32	2
<i>Phellodendron amurense</i> Rupr.	3200	1000	0.23	43.43	79.53	0.23	−32	8
<i>Quercus mongolica</i> Fisch. ex Turcz.	3100	1100	0.32	60.27	87.92	0.51	−34	9
<i>Ulmus davidiana</i> var. <i>japonica</i> (Rehder) Nakai	2700	900	0.35	63.62	105.35	0.18	−33	5
<i>Acer mono</i> Maxim.	3200	1000	0.52	62.10	89.69	0.23	−32	2
<i>Betula costata</i> Trautv.	1900	700	0.35	63.62	105.35	0.19	−35	4
<i>Betula dahurica</i> Pall.	3100	600	0.75	74.52	118.67	0.49	−35	4
<i>Tilia amurensis</i> Rupr.	2400	800	0.40	67.36	87.65	0.23	−33	2
<i>Betula platyphylla</i> Suk.	3100	600	0.75	74.52	118.67	0.41	−38	4
<i>Populus davidiana</i> Dode	3000	700	0.66	78.77	146.52	0.33	−34	7

DMX, degree day maximum, which is counted above 5 °C (d·°C); DMN, degree day minimum, which is counted above 5 °C (d·°C); B2 and B3 are growth parameters of Richard function; G scales the growth rate; D3, the proportion of growing season species can withstand drought; FT, minimum January temperature species can withstand (°C); TL, leaf litter type.

2.4. LANDIS PRO Model and Parameterization

LANDIS, a raster-based forest landscape model, records species distribution (presence or absence) and abundance (density and basal area) by age cohorts on each pixel. LANDIS simulates population dynamics, seed dispersal, and anthropogenic disturbances (such as harvest) with flexible temporal and spatial resolutions of 1 to 10 years and 10 to 500 m [20,23]. Population dynamics are mainly driven by species' ecological traits and include growth, fecundity, competition, colonization, and mortality. Individual growth is represented by the relationship between age and diameter at the breast height. LANDIS simulates fecundity comprising seed germination and resprouting to consider species birth or recruitment. Competition is controlled by the growing space occupied (GSO), and the larger GSO indicates stronger competition. Once the GSO reaches the maximum, self-thinning will be initiated, which releases some growing space and alleviates competition in the stand. When species seeds or resprouting reach a pixel, it checks that species shade tolerance, the GSO, and the SEP to determine whether it can be colonized. LANDIS considers the mortality induced by competition, disturbance, and exceeding the maximum longevity. Seed dispersal is simulated by the location and abundance of seed provenance and dispersal distance, which establishes spatial interaction among pixels. Disturbance such as harvest is conducted in specific management units based on different harvest strategies (e.g., harvest type and proportion, species preference).

We parameterized LANDIS with the temporal and spatial resolutions of 10 years and 100 m. We generated the species composition map based on the forest stand map detailing the species composition and abundance, and the inventory data provided the age information. We introduced how to divide forest landscapes into eight land types in Section 2.3. We derived the stand map and management area map based on the boundaries of forestry management and forest function type described by the forest stand map, respectively. Based on the previous study, we parameterized the species' biological traits in Table 2 [10,11,24]. The growth curve, the relationship between the number and width of the tree ring, was derived from the studies in this region [11,24]. The SEP and MGSO were calculated by the ecosystem process model LINKAGES in Section 2.3 [16,25]. Before executing all simulation scenarios, we also verified the total basal area predicted by LANDIS with forest inventory data and ensured no significant difference between them [10]. We considered the effect of seed harvesting on the natural regeneration of *Pinus koraiensis* by reducing its number of potential germination seeds (NPGS) and gained the outputs from LANDIS including its basal area and the abundance of juveniles with ages less than 10 years.

Table 2. The main species' biological traits in the LANDIS model.

Species	MT	LG	ST	MD	MDBH	MSDI	NPGS
<i>Pinus koraiensis</i> Sieb. & Zucc.	40	300	4	150	110	550	20
<i>Picea jezoensis</i> var. <i>microsperma</i> (Lindl.) W.C.Cheng & L.K.Fu and <i>Picea koraiensis</i> Nakai	30	300	4	150	90	600	20
<i>Abies nephrolepis</i> (Trautv.) Maxim.	30	300	4	150	85	650	20
<i>Larix gmelinii</i> (Rupr.) Kuzen.	20	300	2	300	95	650	30
<i>Fraxinus mandshurica</i> Rupr.	30	250	3	300	100	600	25
<i>Juglans mandshurica</i> Maxim.	20	250	2	200	90	650	25
<i>Phellodendron amurense</i> Rupr.	20	250	3	300	95	650	25
<i>Quercus mongolica</i> Fisch. ex Turcz.	20	300	2	200	95	600	20
<i>Ulmus davidiana</i> var. <i>japonica</i> (Rehder) Nakai	20	250	3	800	90	600	25
<i>Acer mono</i> Maxim.	20	200	3	200	60	700	25
<i>Betula costata</i> Trautv.	20	250	3	800	90	650	25
<i>Betula dahurica</i> Pall.	15	150	2	800	50	750	25
<i>Tilia amurensis</i> Rupr.	30	300	3	200	85	650	20
<i>Betula platyphylla</i> Suk.	15	150	1	2000	50	800	30
<i>Populus davidiana</i> Dode	15	150	1	2000	60	800	30

MT, species maturity age (year); LG, species maximum (year); ST, shade tolerance class ranging from 1 to 5, 1 and 5 denote the least and the most tolerance, respectively; MD, maximum dispersal distance (m); MDBH, maximum diameter at breast height (cm); MSDI, maximum stand density index (number of standard trees per hectare, which refers to 25.5 cm tree); NPGS, number of potential germination seeds per mature tree (number/one raster cell).

2.5. Experimental Design

We designed a two-factor experiment for seed harvesting (with or without harvesting) and climate change (historical climate and future climate) to evaluate how seed harvesting and climate change affected the natural regeneration of *Pinus koraiensis* (Table 3), resulting in four types of simulation scenarios, that is, historical climate without harvesting (S_{HN}), historical climate with harvesting (S_{HH}), future climate without harvesting (S_{FN}), and climate with harvesting (S_{FH}). Given the uncertainties of future climate change, we selected the predictions from four GCMs GFDL-CM3, HadGEM2-ES, MIROC5, and MRI-CGCM3 under the RCP8.5 scenario as the future climate scenarios to represent the ranges of climate variables such as temperature, precipitation and so on. The previous investigation found that seed harvesting decreased the seed bank of *Pinus koraiensis* by at least 80% in the mixed *Pinus koraiensis* forests [9,18]. Thus, we reduced its NPGS by 80% in the LANDIS simulations to consider the effect of seed harvesting. We simulated each scenario of seed harvesting and climate change in combination with five replicates to account for simulation stochasticity. Fifty simulations were conducted (2 seed harvesting scenarios \times 5 climate scenarios \times 5 replicates). We simulated changes in the natural regeneration of *Pinus koraiensis* under each scenario with the same initial stand condition by LANDIS in the next 150 years.

Table 3. Factorial experiment.

Climate Scenarios	Seed Harvesting Scenarios	
	Without Harvesting	With Harvesting
Historical climate observation	S_{HN}	S_{HH}
Future climate RCP8.5	S_{FN}	S_{FH}

S_{HN} , historical climate without harvesting; S_{HH} , historical climate with harvesting; S_{FN} , future climate without harvesting; S_{FH} , climate with harvesting.

2.6. Data Analysis

We used the abundance of *Pinus koraiensis* juveniles with ages less than 10 years to represent its natural regeneration since the abundance of seedlings or saplings in each size class strongly depended on the quantities of seedlings or saplings in the next smaller size class at the same site, which reflected demographic inertia [26]. We compared the differences in the natural regeneration by the ANOVA and the Duncan test to determine how its regeneration changed with the simulation in the short- (years 0–50), medium- (years 60–100), and long-term (years 110–150), respectively. We calculated the change rate of the abundance of juveniles and basal area of all age cohorts to represent the regeneration capacity of *Pinus koraiensis* at the landscape scale since the density of juveniles was significantly related to its basal area [27]. We derived the regeneration capacity from the abundance of juveniles and basal area predicted by seed harvesting and climate combination scenarios in 50, 100, and 150. We selected the spatial distribution of regeneration of *Pinus koraiensis* at the years 50, 100, and 150, and we calculated the mean values within each 1 km zones along the longitudinal direction to reflect how seed harvesting and climate change affected its migration into high-latitude regions. We quantified the seed harvesting effect (SHE), climate change effect (CCE), and their interactive effect (ITE) and combined effect (CBE) based on the relative change in the abundance of juveniles between the scenarios in the short-, medium-, and long-term by Equation (1) to evaluate how the four effects alone and in synergy impacted on the regeneration of *Pinus koraiensis*. We calculated the magnitudes of the SHE, the CCE, and the CBE by the relative change in the abundance of *Pinus koraiensis* juveniles between the scenario S_{HH} and S_{HN} , between the scenario S_{FN} and S_{HN} , and between the scenario S_{FH} and S_{HN} , respectively. We calculated the magnitude of the ITE by the CBE subtracting the additive effect (ADE) defined as the sum of the SHE and the CCE [16,28].

$$\frac{S_1 - S_2}{S_2} \times 100 \quad (1)$$

where S_1 and S_2 represented different scenarios of seed harvesting and climate change combination separately.

3. Results

3.1. Temporal Variations in the Natural Regeneration of *Pinus koraiensis*

The abundance of *Pinus koraiensis* juveniles increased under alternative scenarios of seed harvesting and climate change combination over the simulation (Figure 2). The differences in the abundance of *Pinus koraiensis* juveniles significantly increased with the simulation. The maximum difference of 1, 8, and 26 stems/ha occurred separately in the short-, medium-, and long-term. Seed harvesting significantly decreased the abundance of juveniles and the diminishing magnitude increased over the simulation, irrespective of climate change. Compared with the excluding harvesting scenario, seed harvesting reduced *Pinus koraiensis* juveniles by 1, 14, and 18 stems/ha under the historical climate (S_{HN} , S_{HH}), and diminished by 1, 17, and 24 stems/ha under the future climate (S_{FN} , S_{FH}) in the short-, medium-, and long-term, respectively. In comparison with the historical climate scenario, climate change increased *Pinus koraiensis* juveniles by 1, 4, and 8 stems/ha when excluding seed harvesting (S_{FN} , S_{HN}), and increased by 1, 1, and 2 stems/ha under seed harvesting (S_{FH} , S_{HH}) in the short-, medium-, and long-term separately.

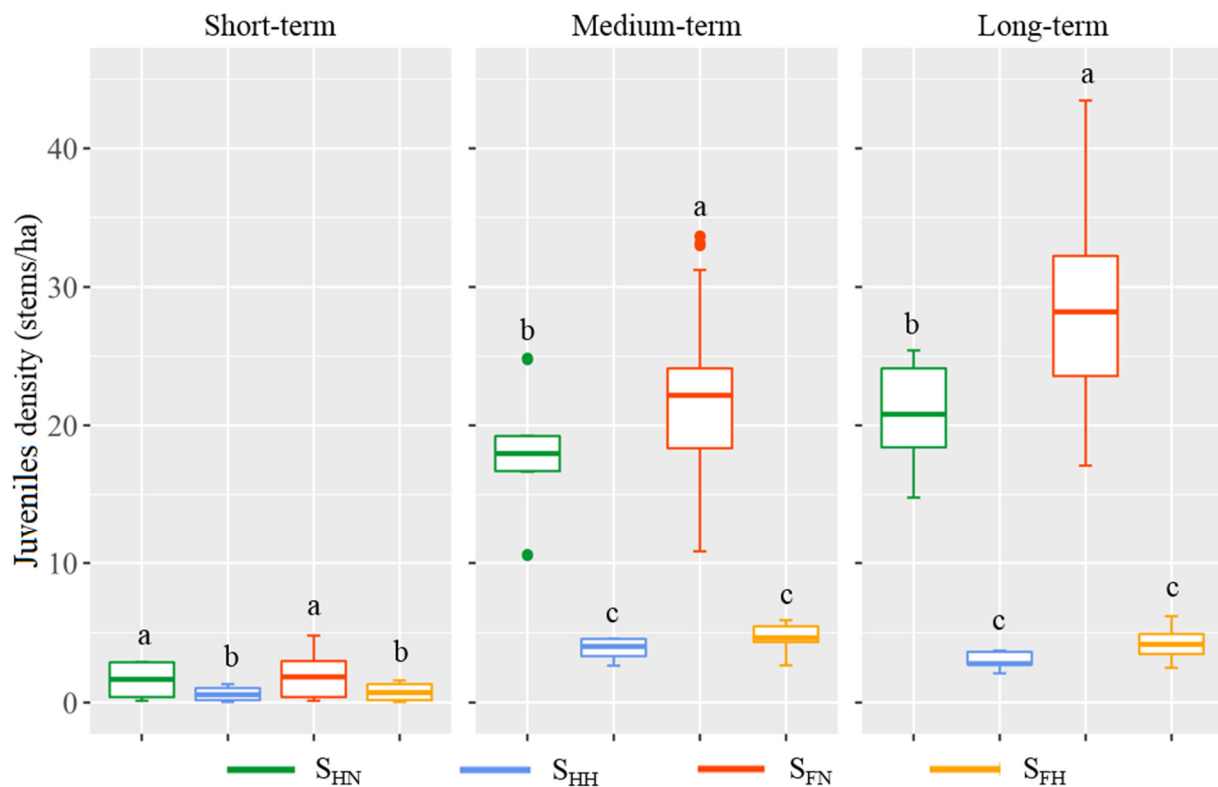


Figure 2. The abundance of *Pinus koraiensis* juveniles under different scenarios of climate and seed harvesting combinations at the whole region scale in the short, medium, and long term, respectively. Different letters displayed significant differences at the 0.05 level among scenarios as determined by the ANOVA and the Duncan test. S_{HN}, historical climate without harvesting; S_{HH}, historical climate with harvesting; S_{FN}, future climate without harvesting; S_{FH}, climate with harvesting.

3.2. Variations in the Natural Regeneration Capacity of *Pinus koraiensis*

Seed harvesting dramatically reduced the regeneration capacity of *Pinus koraiensis* (change rate between the abundance of *Pinus koraiensis* juveniles and the basal area of all age cohorts) under both historical climate and future climate, and the decreased magnitudes of regeneration capacity increased over time (Figure 3). Compared with excluding harvesting, seed harvesting diminished the regeneration capacity of *Pinus koraiensis* by 16.2, 27.7, and 29.3 stems/m² under the historical climate scenario and averagely decreased by 16.5, 29, and 31.8 stems/m² under the future climate scenarios at the years 50, 100, and 150, respectively. In contrast to historical climate, climate change increased the regeneration capacity of *Pinus koraiensis* by 0.2, 0.1, and 1.3 stems/m² under seed harvesting scenarios and increased by 0.5, 1.4, and 3.8 stems/m² under excluding harvesting scenarios at the years 50, 100, and 150 respectively.

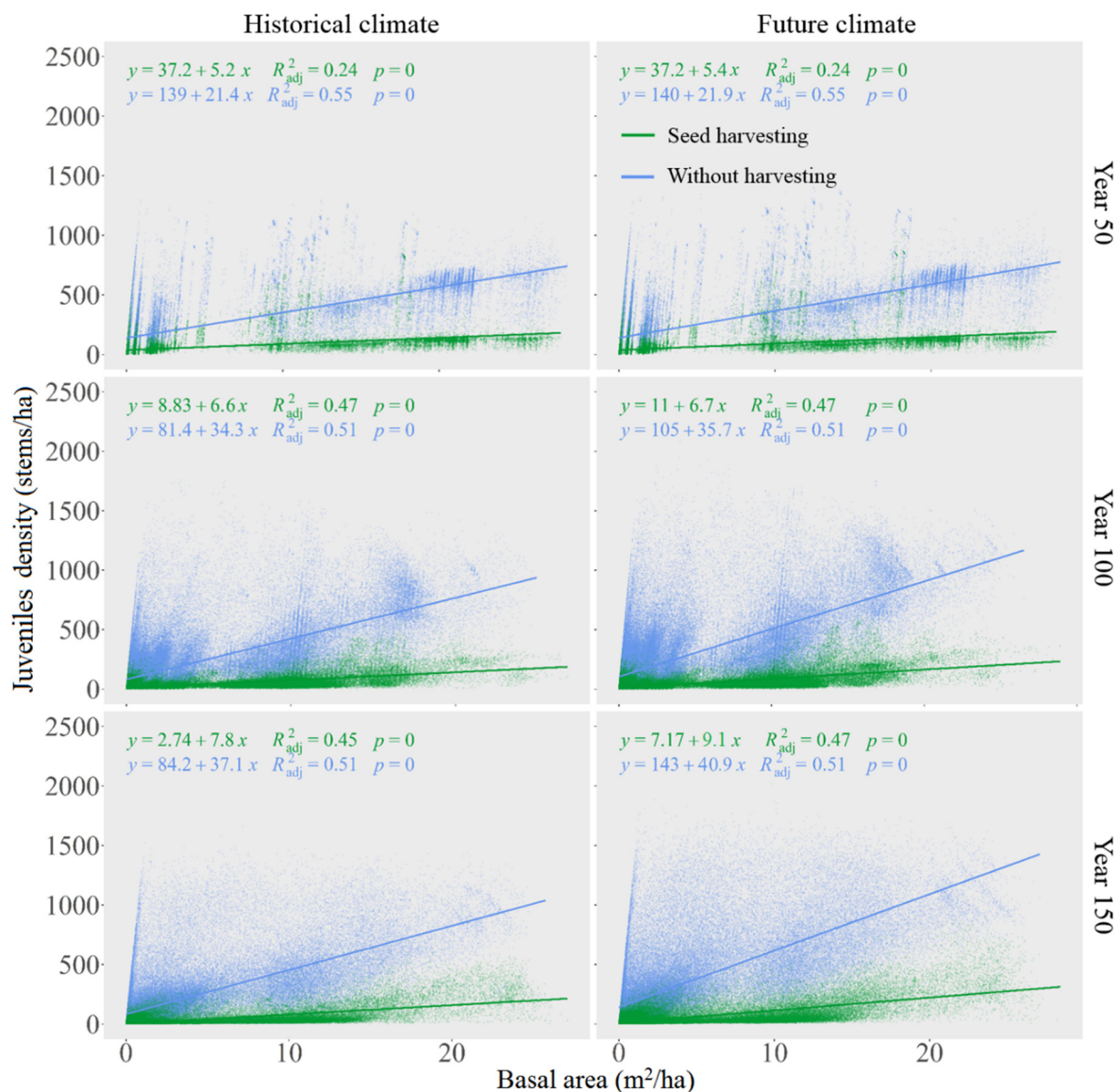


Figure 3. The relationship between the abundance of *Pinus koraiensis* juveniles and its basal area at the years 50, 100, and 150 under the different scenarios of seed harvesting and climate change combination.

3.3. Spatial Changes in the Natural Regeneration of *Pinus koraiensis*

The area and quantity of *Pinus koraiensis* juveniles increased with the simulation under the four scenarios of seed harvesting and climate change combination (Figure 4a,b). The leading edge of *Pinus koraiensis* juveniles migrated into high-latitude regions irrespective of combination scenarios. Compared with the seed harvesting scenario (S_{HH}) and the excluding harvesting scenario (S_{HN}) under historical climate, it was found that seed harvesting decreased the *Pinus koraiensis* juveniles by 142, 147, and 217 stems/ha on average in the whole region at the years 50, 100 and 150 separately. In contrast to the future climate scenario (S_{FN}) and the historical climate scenario (S_{HN}) excluding harvesting, climate change increased the *Pinus koraiensis* juveniles by 11, 35, and 75 stems/ha on average throughout the region at the years 50, 100 and 150, respectively (Figure 4a). Seed harvesting reduced the *Pinus koraiensis* juveniles throughout the study area regardless of climate change but had regional differences at different periods (Figure 4b). Seed harvesting had an unobvious impact on the juveniles in the *Pinus koraiensis* distribution with a latitude above 48.5° N at the year 50 but had evident effects at the years 100 and 150.

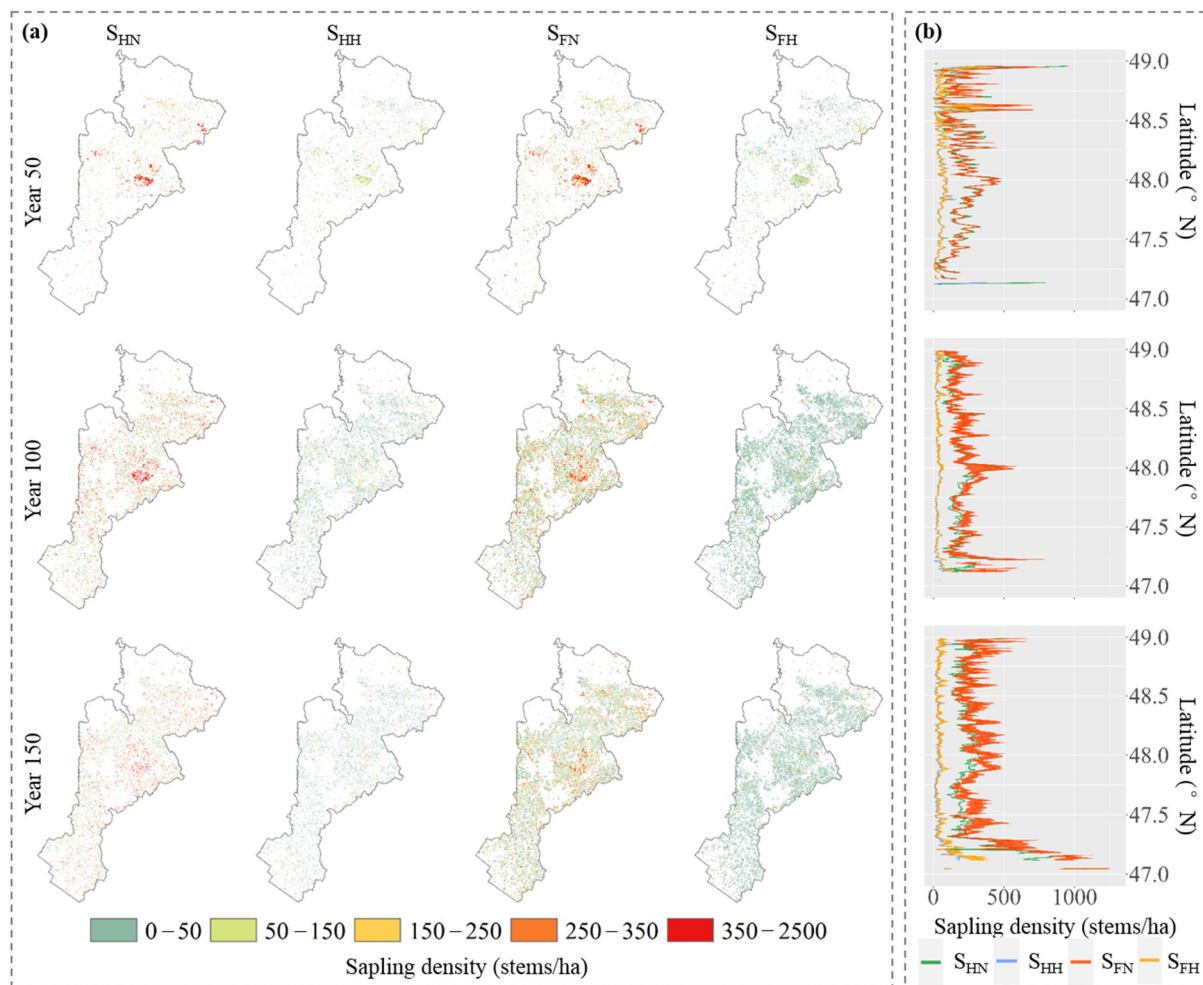


Figure 4. The spatial distribution of the abundance of *Pinus koraiensis* juveniles under the different scenarios of climate and seed harvesting combinations in 50, 100, and 150 (a); The spatial distribution of the abundance of *Pinus koraiensis* juveniles along the longitudinal direction under the different scenarios of seed harvesting and climate change combination in 50, 100 and 150 (b). Error bands represented one standard deviation of the abundance of *Pinus koraiensis* juveniles among scenarios of seed harvesting and climate change combinations. S_{HN}, historical climate without harvesting; S_{HH}, historical climate with harvesting; S_{FN}, future climate without harvesting; S_{FH}, climate with harvesting.

3.4. Effects of Seed Harvesting and Climate Change

The adverse effects of seed harvesting on the natural regeneration of *Pinus koraiensis* were always dominant, and the average effect magnitudes were -61.1% , -78.4% , and -85.7% in the short-, medium, and long-term, respectively (Figure 5). The favorable effects of climate change were 16.5% , 20.9% , and 38.2% in the short-, medium, and long term separately. There was an interactive effect between seed harvesting and climate change, and the interaction negatively impacted the regeneration of *Pinus koraiensis*. The interactive effect increased over the simulation and the average effect magnitudes were -10.1% , -16.2% , and -32.0% in the short-, medium, and long-term, respectively. Climate change and seed harvesting combinedly reduced the regeneration of *Pinus koraiensis*. The magnitudes of the combined effects were -54.7% , -73.8% , and -79.5% in the short-, medium- and long-term, respectively. Climate change failed to offset the unfavorable effect of seed harvesting. The effect sizes of climate change were 44.6% , 57.5% , and 47.5% lower than the absolute values of seed harvesting separately in the short-, medium- and long-term.

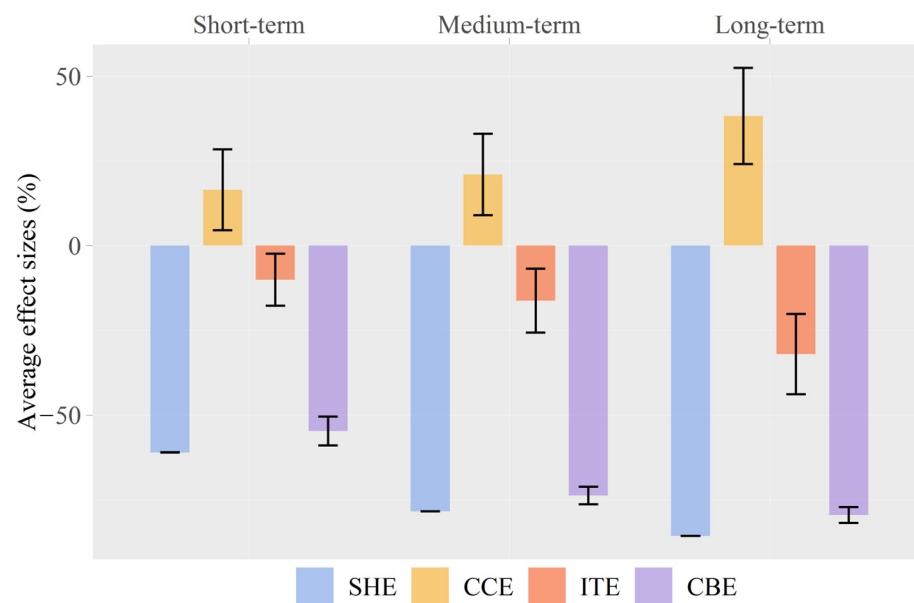


Figure 5. The average effect sizes of seed harvesting (SHE), climate change (CCE), and their interaction (ITE) and combination (CBE) on *Pinus koraiensis* regeneration in the short-, medium-, and long-term, respectively. Error bars of SHE represented one standard deviation of five replicates, and the remaining bars represented one standard deviation of the combination scenarios of four future climates projected by GCMs and five replicates (20 simulations, 4 climate scenarios \times 5 replicates).

4. Discussion

Our results show that seed harvesting aggravates the poor natural regeneration of *Pinus koraiensis*, which generally is restricted by the light availability in Northeast China [5,29,30]. Seed harvesting has significantly decreased the natural regeneration of *Pinus koraiensis*, and the negative effect increases with forest succession. However, we find the differences in the short-term are small but large in the medium- and long-term between the scenarios with and without seed harvesting (Figure 2), which indicates seed harvesting has a lagging effect on the natural regeneration of *Pinus koraiensis* that is determined by its mature age. Although seed harvesting cannot cause the death of the existing *Pinus koraiensis*, it reduces the provenances and further decreases the abundance of *Pinus koraiensis* seedlings at the landscape scale, resulting in the loss of adult trees in the future. Decreases in the adult trees of *Pinus koraiensis* will further diminish its seed banks and exacerbate its poor regeneration. The previous studies at the plot or stand scale find that seed harvesting significantly reduces the seed and seedling banks of *Pinus koraiensis* [4,9,17]. Still, they fail to consider the effect of seed dispersal that may alleviate the adverse effect induced by seed harvesting. We apply a forest landscape model and simultaneously consider the effects of seed harvesting and dispersal in this study, which can provide more accurate results at the landscape scale from the methodology perspective. Our results indicate that the pressures from the continued predatory seed harvesting and the poor natural regeneration of *Pinus koraiensis* increase the challenges for restoring the secondary forests to the primary mixed *Pinus koraiensis* forests at the landscape scale [2].

Our results demonstrate climate change with the warming and wetting trends promotes the natural regeneration of *Pinus koraiensis*, and the favorable effect increases with the simulation. The previous study finds warm and wet climate combinations promote seed germination which supports our finding [31]. Still, a warm and dry climate combination has an inhibition effect which agrees with a dendrochronological study that drought induced by climate change restricts the growth of *Pinus koraiensis* at the trailing edge and its young age cohort [14]. There are regional differences in the response of *Pinus koraiensis* to a warming climate. The previous study has shown that rising temperature increases the growth of *Pinus koraiensis* at the leading edge, but decreases the growth in the midwestern

regions and has little effect at the trailing edge [32]. Considering the differences in these responses and the uncertainties of future climate change, we suggest that multiple climate models should be integrated when investigating the responses of tree species to climate change in order to capture their diverse responses.

We find that seed harvesting decreases the regeneration capacity of *Pinus koraiensis* and hinders its migration at the leading edge irrespective of climate conditions. Generally, the stand with a more basal area of *Pinus koraiensis* can provide more seed provenance to germinate [27], consistent with our results that the abundance of juveniles increases with the rising basal area of *Pinus koraiensis* at the landscape scale (Figure 3). Regeneration dynamics is the key process that determines species shifts induced by climate change [33]. Seed harvesting reduces the opportunities for *Pinus koraiensis* recruitments, especially at the leading edge with low levels of dominance and the seed bank of *Pinus koraiensis*. Our results show the adverse effect of seed harvesting at the leading edge is unobvious in the short-term (year 50), but evident in the medium- and long-term (years 100 and 150) (Figure 4). We assume that the low dominance and seed bank of *Pinus koraiensis* results in a lagging effect of seed harvesting on its shift. Recent studies show that tree species migration fails to keep up with the step of climate change [13,16,34], while seed harvesting further impedes the migration of *Pinus koraiensis* to high-latitude regions, which is unfavorable for altering its distribution to adapt to the future climate.

Our results indicate the interactive effects between seed harvesting and climate change on the natural regeneration of *Pinus koraiensis*. The interaction has the same direction as seed harvesting and thereby exacerbates the contraction of recruitments induced by seed harvesting. It is since that climate change, under the circumstances that seed harvesting markedly obstructs the regeneration of *Pinus koraiensis*, benefits the recruitment of the other species, such as *Picea koraiensis* and *Picea jezoensis* and *Abies nephrolepis*, with similar ecological niche to *Pinus koraiensis* [10]. The effect of seed harvesting alone predominates throughout the simulation, followed by climate change alone and the interaction between them (Figure 5). We find that seed harvesting, climate change, and their interaction combinedly have adverse effects on the natural regeneration of *Pinus koraiensis*, and the positive effect of climate change fails to counteract the negative effect of seed harvesting. The previous study finds there is an interaction between climate change and timber harvesting on species distribution, emphasizing the interaction between multiple factors [16]. Our results also indicate the interactive effect between seed harvesting and climate change is comparable to climate change alone. Given the importance of interaction, we also suggest multiple drivers of recruitment changes should be assessed concurrently since the interactive effect is unable to be determined when the individual effect is considered independently.

Future forest management should consider silvicultural treatments, such as thinning from below and artificial plantation combinations, to protect the mother tree of *Pinus koraiensis* and promote its regeneration. A recent study finds that predatory seed harvesting has a long-lasting effect and decreases the dominance of *Pinus koraiensis* in the long term [10]. It is necessary to reduce the intensity and rotation of seed harvesting to ensure sufficient provenance to maintain the regeneration of *Pinus koraiensis* in the future. Although *Pinus koraiensis* seedlings are shade tolerant, their need for light increases with age [35]. Previous studies have shown that understory light availability limits the growth and survival of *Pinus koraiensis* seedlings [5,29,30] while thinning from below increases light availability by creating forest gaps, promoting the regeneration of shade-tolerant species such as *Pinus koraiensis* [5,36,37]. A previous study finds that the low thinning and slash burning treatment enhances initial Spanish black pine seedling recruitments [38]. The previous study shows thinning from below promotes *Pinus koraiensis* growth and increases the abundance of its juveniles at the landscape scale [11]. Artificial treatments such as direct seeding or seedling planting can be applied to promote the regeneration of *Pinus koraiensis* [39,40]. A recent study found that planting seedlings have a higher survival rate than direct seeding. However, the high costs of planting seedlings greatly restrict its application to a large spatial extent [39], while direct seeding may have more potential. Therefore, compositing

these treatments may provide effective ways to promote the regeneration of *Pinus koraiensis*, which is of great significance for maintaining its dominance and restoring the primary mixed *Pinus koraiensis* forests.

Our study also has some limitations. *Pinus koraiensis* mainly relies on rodents that carry and bury seeds to achieve the process of seed dispersal [39]. Since seed harvesting directly reduces the food sources for these animals and may decrease their population size, which in turn will diminish the abundance of the buried seeds and thus adversely impact the natural regeneration of *Pinus koraiensis* [10]. We fail to take rodent population dynamics into account, which increases the uncertainties of the simulation. The seed yield of *Pinus koraiensis* has obvious inter-annual fluctuation [41], which alters the behavior of rodents and the seed dispersal process [37], and ignoring these impacts increases the uncertainties of *Pinus koraiensis* recruitment at the landscape scale. Generally, the natural regeneration of *Pinus koraiensis* occurs in forest gaps [42,43]. Wind disturbance naturally creates forest gaps in the forest landscape; we exclude the effects of wind on the regeneration of *Pinus koraiensis* in this study, which increases the uncertainties of prediction. Additionally, the variations indirectly induced by climate change in intensity, extent, and rotation of wind also contribute to the uncertainties [43]. Despite these shortcomings, our study still highlights the separate and interactive effects of seed harvesting and climate change on the regeneration of *Pinus koraiensis*, which provides an important reference for promoting the regeneration and dominance of *Pinus koraiensis* and restoring the mixed *Pinus koraiensis* forests from a landscape perspective.

5. Conclusions

We assessed and quantified how seed harvesting and climate change impacted the natural regeneration of *Pinus koraiensis* at the landscape scale by coupling an ecosystem process model with a forest landscape model in this study. We found that seed harvesting significantly exacerbated the poor natural regeneration of *Pinus koraiensis*. Seed harvesting evidently decreased the regeneration capacity of *Pinus koraiensis* and delayed its migration into the high latitude regions to adapt to future climate. We concluded seed harvesting always was dominant throughout the simulation, and climate change failed to neutralize the adverse effect of seed harvesting. Additionally, we found that the interactive effect between seed harvesting and climate change approached the magnitude of climate change alone, which indicated the interaction almost offset the positive effect of climate change. We suggest future management should decrease the intensity and rotation of seed harvesting and promote the regeneration and restoration of the primary mixed *Pinus koraiensis* forests through silvicultural treatments such as thinning from below, seedling planting, or direct seeding.

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