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Evaluating the Legacy Effects of the Historical Predatory Seed Harvesting on the Species Composition and Structure of the Mixed Korean Pine and Broadleaf Forest from a Landscape Perspective

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Abstract: Adequate seed provenance is an important guarantee for the restoration of the mixed Korean pine *(Pinus koraiensis)* and broadleaf forest (MKPBF). However, the commercial harvest exclusion in natural forests has led to a sharp decline in economic income from timber. Given the economic value of Korean pine seeds, predatory seed harvesting (PSH) has become increasingly serious in the past 20 years and has significantly reduced the seed and seedling bank, which might seriously threaten the restoration and sustainable management of the MKPBF. How the historical PSH has affected the future of the MKPBF is unclear at the landscape scale. In this study, we quantified the effects of seed harvesting at the landscape scale by a forest landscape model LANDIS PRO, and then assessed the legacy effects of the historical PSH on the composition and structure of the MKPBF in the Xiaoxing'an Mountains, Northeast China. Our results showed that the historical PSH decreased the Korean pine basal area of all age cohorts, with an average decrease of 0.06 to 0.19 m^2 ha^{-1} but insignificantly altered the age structure diversity of Korean pine throughout the simulation. Our results indicated that the historical PSH remarkably decreased the dominance of Korean pine by 11.1%, but significantly increased the dominance of spruce (*Picea koraiensis* and *Picea jezoensis*) and fir *(Abies nephrolepis*) by 3.8% and 4.5%, respectively, and had an insignificant effect on the other tree species over the simulation. We found that the historical PSH evidently changed the succession trajectories of the disturbed stands, which would result in the transition from the succession pattern dominated by Korean pine to that dominated by spruce and fir. The historical PSH decreased the importance value of Korean pine by 12.2% on average but increased it by 5.1% and 6.0% for spruce and fir, respectively, and resulted in an average 33.2% increase in the dissimilarity index compared with the initial state during the whole simulation period. Future forest management should strictly limit the intensity and rotation of seed harvesting to protect the seed provenance of Korean pine and consider how to ensure the recovery and sustainable management of the MKPBF through direct seeding or seedling planting.

Keywords: seed harvesting; forest landscape model; mixed Korean pine and broadleaf forest

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1. Introduction

The mixed Korean pine (*Pinus koraiensis*) and broadleaf forest (MKPBF) provides important ecosystem services, such as timber and seed products [1,2]. However, the primary MKPBF has degraded into a secondary forest due to excessive harvesting in the past half of the century; meanwhile, the abundance of the dominant species Korean pine has dropped sharply. The Chinese government implemented the Natural Forest Conservation Program (NFCP) in 1998 and the Commercial Harvest Exclusion Policy (CHEP) in 2014 to increase forest stock and restore the MKPBF [3]. Although the above measures restored forest timber stock, they resulted in a significant reduction in income for local residents [4,5]. In order to compensate for the decreasing income from timber harvest, Korean pine seed was intensively harvested because of its high economic value. A previous study showed that the predatory seed harvesting (PSH) declined seed abundance and further hindered Korean pine regeneration, which increased the challenges of forest restoration [6].

The key issue of restoring the MKPBF was to promote Korean pine regeneration, which was mediated by seed sources [7,8]. Seed harvesting, with a long history, is an important anthropogenic disturbance that reduces Korean pine seed abundance in the MKPBF [9–11]. Especially after the NFCP, the effect of PSH was serious in the general ecological welfare forests and the commercial forests due to the decrease in timber income [4,6,11,12]. At present, the PSH has lasted for about 20 years in these regions. Although the PSH had had a nonobvious influence on the Korean pine forest at the landscape scale, it has caused a lagging effect on its regeneration for about 20 years. Korean pine was characterized by poor natural regeneration [13], which may be exacerbated by the PSH. A recent study found that provenance limitations, which were caused by the disappearance of Korean pine due to the historical disturbance and caused by the seed harvesting, reduced the effectiveness of seed dispersal, and thereby decreased the chance of regeneration of young Korean pine in the secondary forest [14]. It remained unknown whether the adverse effect of the historical PSH on Korean pine young age cohort would be transferred to older age cohorts and would further reduce the age structure diversity of Korean pine.

Disturbance would alter the interspecific relationship between Korean pine and its associated tree species in the MKPBF. Korean pine was often associated with fir (*Abies nephrolepis*), spruce (*Picea koraiensis and Picea jezoensis*), Amur linden (*Tilia amurensis*), Manchurian ash (*Fraxinus mandschurica*), Ribbed birch (*Betula costata*) and Mongolian oak (*Quercus mongolica*), and formed a typical Korean pine mixed forest [15]. Korean pine and its associated tree species were both symbiotic and competitive. The PSH would increase the challenges for Korean pine regeneration in the disturbed forest landscape, but it would indirectly promote the regeneration of its associated tree species, which might change the species composition of the MKPBF in the long term and might even alter its succession trajectory. A previous study based on gap model found that once there was no Korean pine provenance, the successional trajectory of forest would change to the mixed broadleaf forest rather than the MKPBF [16]. Currently, it is unclear whether such a cumulative anthropogenic disturbance would significantly change the species composition and succession trajectory of the MKPBF.

It was challenging to assess the legacy effects of seed harvesting on the MKPBF at the landscape scale. Seed harvesting, a landscape process, could synergize with seed dispersal at the landscape scale and competition at the stand scale to affect Korean pine regeneration and further impact the future of the MKPBF. To date, most of the studies focused on investigation and monitoring at the plot or stand scale [6,10–12]. Such research reflects the adverse effect of seed harvesting on some trees or stands at the individual and stand scales, but it is hard to clarify its effect on the MKPBF over a larger temporal and spatial scale. However, the forest landscape model could simulate the synergistic effects among forest population dynamics, seed dispersal and timber harvesting on the MKPBF at the large temporal and spatial scales [4,17–19]. The previous investigation found that the PSH for 20 years decreased the seedling bank by at least 80% [12], and we assumed that the relationship between seed harvesting and seedling bank would also hold in the future. We attempted to simulate harvesting Korean pine seedlings by the forest landscape model to consider the effect of seed harvesting. Thus, the forest landscape model provided a feasible tool to evaluate the effect of seed harvesting at the landscape scale.

In this study, we assessed how the PSH in the past 20 years would influence the species composition and structure of the mixed Korean pine and broadleaf forest in the

Xiaoxing'an Mountains at the landscape scale through a forest landscape model, LANDIS PRO. Specifically, we addressed the following question: (1) whether the negative effect of the historical PSH on Korean pine young age cohort would be delivered to older age cohorts, and then would decrease the age structure diversity of Korean pine; (2) the dominance of which tree species would be promoted by the historical PSH; and (3) whether the historical PSH would change the succession trajectory dominated by the MKPBF into the broadleaf forest or the other mixed coniferous and broadleaf forest. We attempted to evaluate the long-term effect of seed harvesting on the MKPBF at the landscape scale by LANDIS PRO and provided a new view for quantifying its effect on forest.

2. Materials and Methods

2.1. Study Area

The study area is located in the Xiaoxing'an Mountains, with a longitude and latitude range of 127°50′ E to 130°10′ E and 47°05′ N to 49°10′ N, covering an area of about 1.5 million hectares and an altitude between 139 m and 1429 m (Figure 1). This area has a temperate continental monsoon climate, and annual mean temperature, and total precipitation decreases from 1.0 °C and 700 mm in the south to −1.0 °C and 550 mm in the north, respectively. The study area includes eight forestry bureaus and one natural reserve. Overharvesting in the past half century has resulted in the degradation of the primary mixed Korean pine and broadleaf forest (MKPBF) to a secondary forest, and the current stand is dominated by a middle-age forest. The major tree species are listed in Table 1. Since the Natural Forest Conservation Program (NFCP) in 1998, forests in this region have been divided into the special ecological welfare forests (SEWFs), the general ecological welfare forests (GEWFs), and the commercial forests (CFs) for classified management [5]. We will parameterize the management area map required for LANDIS according to these three forest types in the Section 2.2. After 2014, commercial harvest was excluded in the area [3]. At present, the seed harvesting of Korean pine is an important human disturbance in the GEWFs and the CFs.

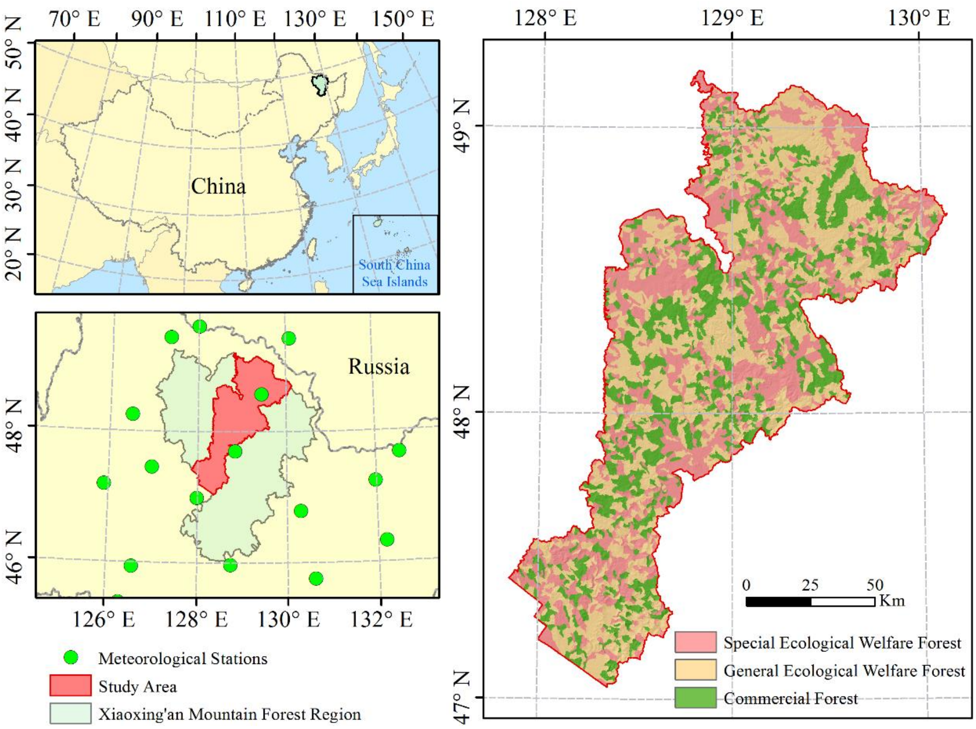

Figure 1. Geographical location and three categories of management zones of the study area.

Table 1. The main species biological traits adapted from liu et al., 2020 [20].

Species	MT	LG	ST	MD	MDBH	MSDI	NPGS
Korean pine, *Pinus koraiensis*	40	300	4	150	110	550	20
Korean spruce, *Picea koraiensis and Picea jezoensis*	30	300	4	150	90	600	20
Khingan fir, *Abies nephrolepis*	30	300	4	150	85	650	20
Larch, *Larix gmelinii*	20	300	2	300	95	650	30
Manchurian ash, *Fraxinus mandschurica*	30	250	3	300	100	600	25
Manchurian walnut, *Juglans mandshurica*	20	250	2	200	90	650	25
Amur corktree, *Phellodendron amurense*	20	250	3	300	95	650	25
Mongolian oak, *Quercus mongolica*	20	300	2	200	95	600	20
Black elm, *Ulmus davidiana*	20	250	3	800	90	600	25
Mono maple, *Acer mono*	20	200	3	200	60	700	25
Ribbed birch, *Betula costata*	20	250	3	800	90	650	25
Dahur Birch, *Betula dahurica*	15	150	2	800	50	750	25
Amur linden, *Tilia amurensis*	30	300	3	200	85	650	20
White birch, *Betula platyphylla*	15	150	1	2000	50	800	30
Poplar, *Populus davidiana*	15	150	1	2000	60	800	30

MT, age of tree species sexual maturity (year); LG, mean maximum age of tree species (year); ST, shade tolerance class (including 1–5, 1 and 5 mean 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 is 25.5cm tree); NPGS, number of potential germination seeds per mature tree (number/one raster cell).

2.2. Forest Landscape Model and Parameterization

LANDIS PRO tracked changes in the absence or presence of tree species, and recorded the tree number and basal area by age cohorts on raster cells [18,21]. LANDIS can simulate the effects of population dynamics, seed dispersal, and harvesting on forest composition and structure over large spatial and temporal extents with flexible resolutions. The population dynamics driven by species ecological traits include growth, fecundity, colonization, and mortality (Table 1). Seed dispersal, a spatial process, establishes spatial interaction among different cells [22]. Harvesting is an anthropogenic disturbance, and it could release growing space by thinning from above or below. The input parameters for the LANDIS model contained that the spatial data mainly included a species composition map, management area map, harvest unit map and land-type map, and that the non-spatial data mainly comprised the species biological traits, species establishment probability (SEP), maximum growing space occupied (MGSO), and growth curve. Individual growth was simulated by a growth curve, which was determined by the relationship between age and DBH (diameter at breast height). Fecundity was regulated by seed yield and dispersal. Once the species' SEP exceeded a random number ranging from 0 to 1, and, meanwhile, the growing space occupied (GSO) was less than MGSO on one cell, then the individual colonized there. Competition was triggered once the GSO reached the MGSO, and the mortality induced by competition was simulated based on Yoda's thinning theory, which was characterized as the larger diameter class and the lower mortality rate [23]. Additionally, LANDIS incorporated the mortality caused by disturbances or by excessive maximum longevity [24]. Harvesting was conducted by the management area map and harvest unit map, which provided the boundaries for the harvest event and the minimum harvest unit, respectively.

We considered the effect of seed harvesting on the MKPBF by harvesting a Korean pine young cohort with the temporal and spatial resolutions of 5 years and 100 m. We used the forest inventory data and a stand composition map to generate an initial species composition map, which detailed the species distribution and abundance by age cohort on each pixel. We derived the management area map according to forest function type described in the stand composition map, and the map was divided into three classes. We only simulated seed harvesting in the general ecological welfare forest and commercial forest and excluded it in the special ecological welfare forest. We used the boundaries of the stand composition map to generate a harvesting unit map. We divided this area into eight land types based on elevation, aspect and the ≥10 °C cumulative temperature line, and we assumed SEP and MGSO were the same for a certain land type but different among other land types. We evaluated the SEP and MGSO in different land types on the basis of the outputs from the forest ecosystem process model LINKAGES [20]. We parameterized species' ecological traits based on the previous ones in this region [20,25]. The species growth curve was derived from the previous study and the forest inventory data that described the relationship between the number and width of tree rings [20,25]. We used 94 forest inventory plots in 2010 and extracted the corresponding basal area from the LANDIS output to verify the simulation. We used a scatter plot of inventory basal area with LANDIS output at the 10th year of simulation because the initial year of parameterization was 2000 and conducted a linear fit (Figure 2). There was a significant linear correlation between the inventory basal area and LANDIS output ($p < 0.01$, R2 = 0.57), while the ANOVA result showed no significant difference between the inventory basal area and LANDIS output ($p = 0.17 > 0.05$)

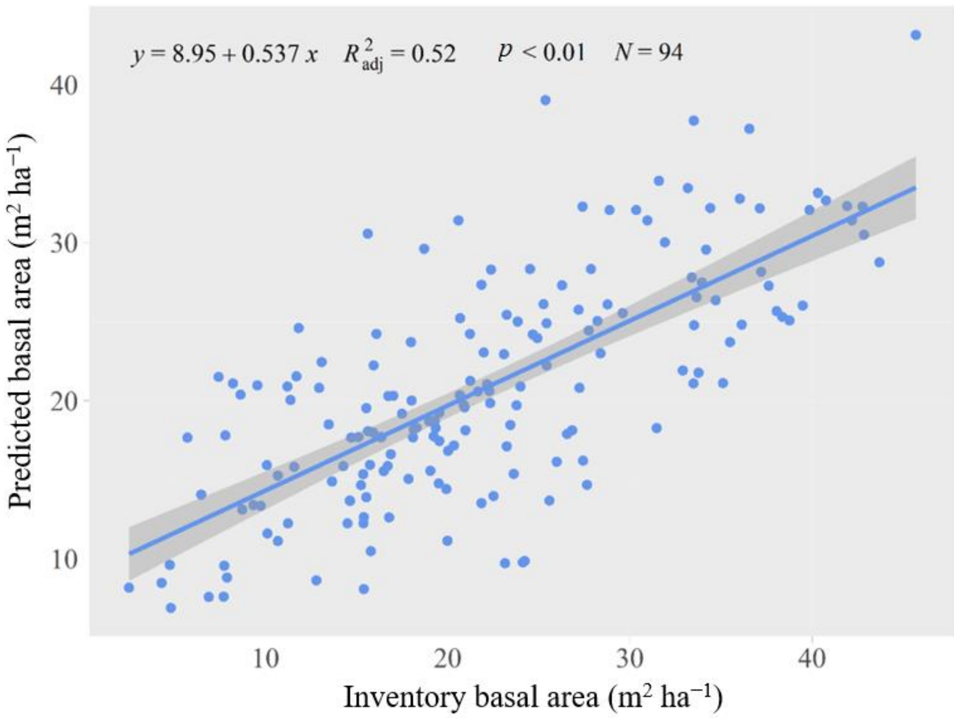

Figure 2. Comparison of the total basal area between forest inventory data and LANDIS outputs in 2010. The grey area indicates the 95% confidence interval of the regression equation.

2.3. Experimental Design

We designed the baseline scenario (BH) and the historical predatory seed harvesting (PSH) scenario (PH) to address how the historical PSH affected the species composition and structure of the mixed Korean pine and broadleaf forest (Table 2). In the BH scenario, we harvested 5% of the distribution area of the Korean pine young cohort every 5 years as a background disturbance to consider the mortality due to animal feeding. A previous inventory found that the PSH lasting for 20 years resulted in the loss of the Korean pine seedling bank by at least 80% [12]. Besides the above background disturbance, we also harvested 80% of the distribution area of the Korean pine young cohort in the first 20 years in the PH scenario to incorporate the effects of the historical PSH. Each scenario was repeatedly simulated five times to account for the uncertainty of the simulation, and the 10 simulations were conducted by LANDIS PRO with the same initial status to predict the variations in the species composition and structure of the MKPBF for 150 years.

Table 2. Forest management scenarios.

Scenarios	Removal Method	Percent Area for Background Harvesting	Percent Area for Historical Predatory Seed Harvesting
Baseline harvest (BH)	Thinning from below	5%	—
Predatory harvest (PH)	Thinning from below	5%	80%

2.4. Data Analysis

We obtained all cells disturbed by the PSH through subtracting the basal area in the BH scenario from that in the PH scenario at each time step for the first 20 years of the simulation. We then summarized the changes in species composition and structure on these cells to reflect the legacy effects of the historical PSH. We divided the Korean pine forest into 5 age cohorts [3], namely young forest (YF, 0–40 years), middle-aged forest (MIF, 40–60 years), near mature forest (NMF, 60–80 years), mature forest (MF, 80–120 years) and aged forest (OGF > 120 years). We counted the basal area of each age cohort output by the two scenarios, respectively, and then used them to calculate the Shannon diversity index in the short-(0–50 years), medium-(55–100 years), and long terms (105–150 years) [26], in order to answer how the historical PSH impacted the age structure of the Korean pine. We calculated the absolute and relative changes in the basal area of tree species under the two scenarios severally to clarify which tree species' dominance the historical PSH improved. Relative changes (increase or decrease) were defined as (PH scenario -BH scenario)/BH scenario*100. We computed the absolute and relative changes in the importance value of tree species in both of the two scenarios, and then we calculated the Bray–Curtis dissimilarity index [27] of the tree species composition in the two scenarios compared with the initial species composition, respectively, to address whether the historical PSH altered the succession trajectory. The importance value (IV), one of the outputs from LANDIS PRO, is described as Equation (1). We used ANOVA to determine whether there were significant differences between the BH scenario and the PH scenario or not. Before executing ANOVA, we tested the normality and variance homogeneity of the data. All data processing and statistical analyses were carried out in R (Version 3.2.2, Vienna, Austria) [28]:

$$IV = \frac{SD}{2 \times TD} + \frac{SBA}{2 \times TBA} \tag{1}$$

where *SD*, *SBA*, *TD* and *TBA* represent species *i* density, species *i* basal area, total density and total basal area, respectively.

3. Results

3.1. Change in the Age Structure of Korean Pine

The historical predatory seed harvesting (PSH) averagely decreased the Korean pine basal area irrespective of age cohorts throughout the simulation. Compared with the baseline scenario (BH), the historical PSH scenario (PH) averagely decreased the basal area of young forest (YF), middle-age forest (MIF), near-mature forest (NMF), mature forest (MF) and old-growth forest (OGF) by 0.06, 0.18, 0.13, 0.19 and 0.15 m^2 ha^{-1}, respectively (Figure 3a,b). The historical PSH insignificantly altered the age structure diversity of Korean pine ($p > 0.05$). In comparison with the BH scenario, the PH scenario increased the age structure Shannon–Wiener index of Korean pine by 0.007 on average, with a relative increase of 0.5% in the short term (Figure 4a), while it averagely reduced the index by 0.009 and 0.012, with relative decreases of 0.6% and 1.1% in the medium and long terms (Figure 4b,c).

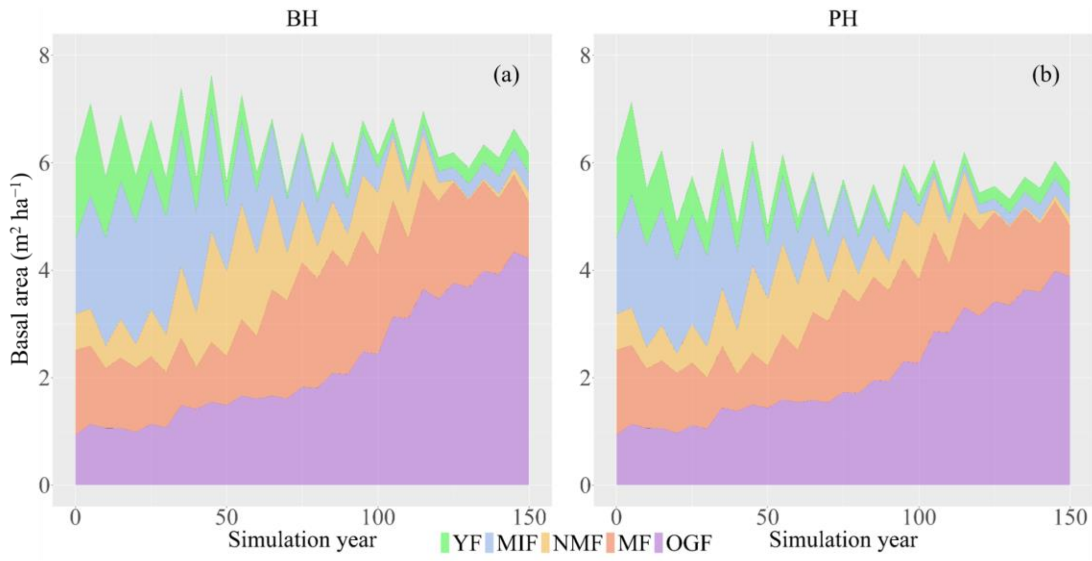

Figure 3. Each age cohort basal area of Korean pine across the simulation period under the BH and PH scenarios. BH, the baseline scenario; PH, the historical PSH scenario. YF, young forest; MIF, middle-age forest; NMF, near-mature forest; MF, mature forest; OGF, old-growth forest.

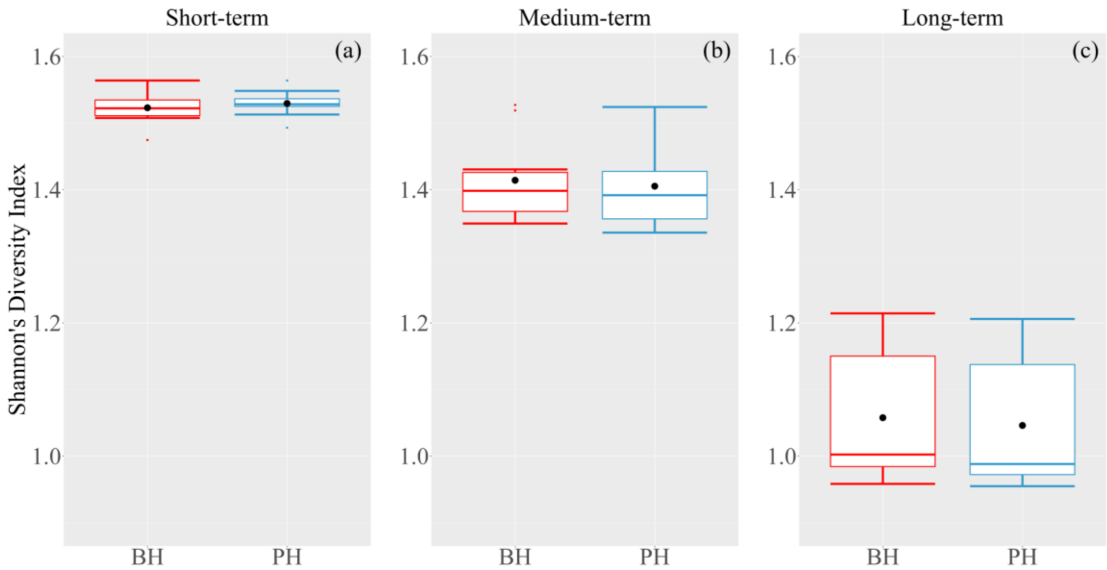

Figure 4. The age structure Shannon–Wiener index of Korean pine in the short-, medium-, and long term under the BH and PH scenarios. The black dots represented the average. The variance referred to the variance among five replicates of Shannon–Wiener index on all cells disturbed by seed harvesting in different terms under the two scenarios, respectively. BH, the baseline scenario; PH, the historical PSH scenario.

3.2. Change in Species Composition

The historical PSH significantly decreased the Korean pine basal area ($p < 0.01$) but remarkably increased spruce and fir ($p < 0.05$) throughout the simulation. In comparison with the BH scenario, the PH scenario averagely decreased the Korean pine basal area by 0.63 m^2 ha^{-1} (Figure 5a), with a relative decrease of 11.1% (Figure 6a), but it increased the basal area of spruce and fir by 0.19 and 0.23 m^2 ha^{-1} (Figure 5b,c), with a relative increase of 3.8% and 4.5% respectively (Figure 6b,c), while it little improved the basal area of larix, ash, walnut, corktree, oak, elm, maple, ribbed birch, dahur birch, linden, white birch, and poplar, with a range from 0.0003 to 0.0536 m^2 ha^{-1} (Figure 5d–o) and a relative change from 0.6% to 2.7% (Figure 6d–o).

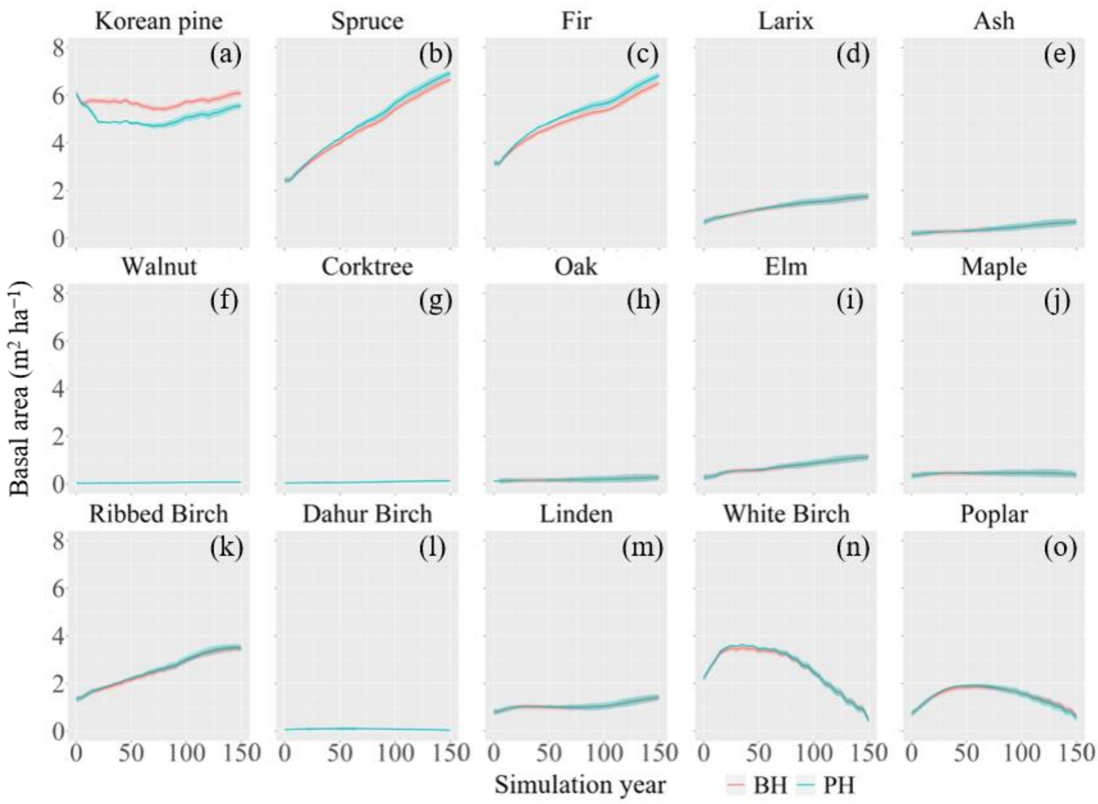

Figure 5. Species basal area under the BH and PH scenarios during the simulation. BH, the baseline scenario; PH, the historical PSH scenario. Error bands indicate one standard deviation of the five replicates.

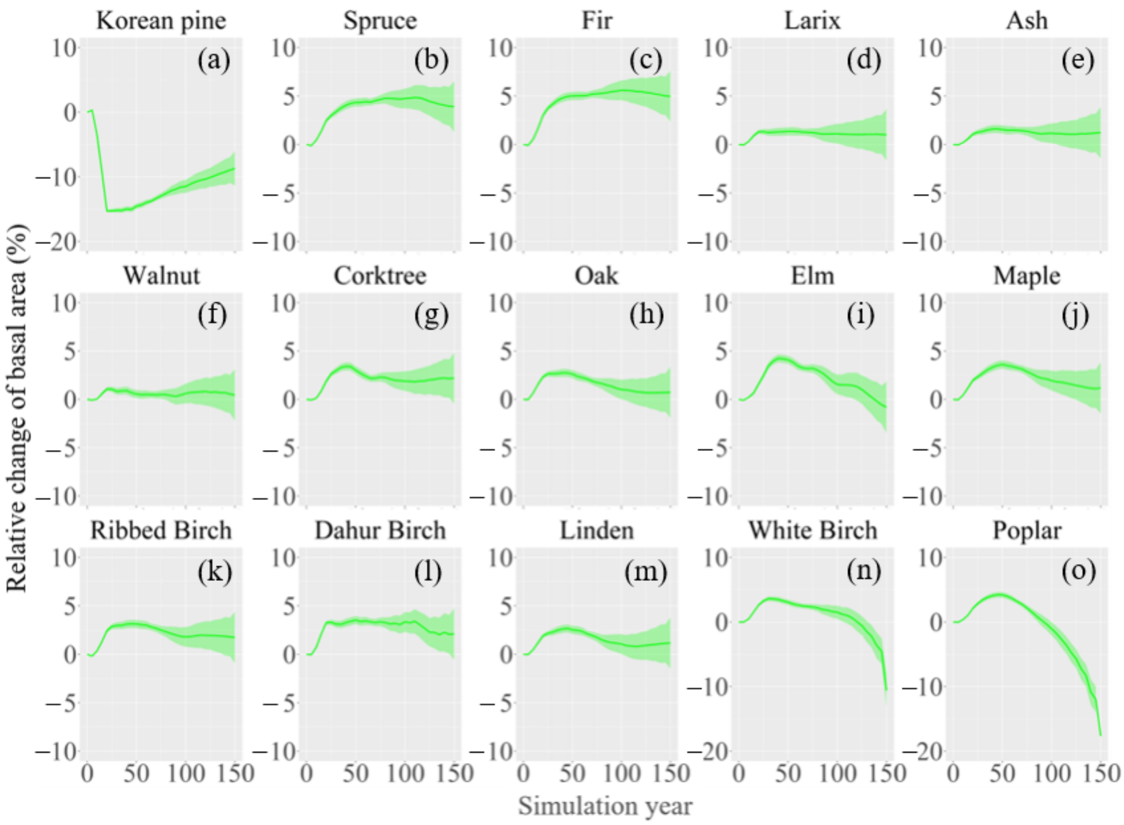

Figure 6. Relative changes in the basal area of each species under the PH scenario compared with the BH scenario over the simulation. Error bands indicate one standard deviation of the five replicates.

3.3. Change in Succession Trajectory

The historical PSH amplified the difference in species composition and significantly altered forest succession trajectory ($p < 0.01$). Compared with the initial year, the Bray–Curtis dissimilarity index of species composition gradually increased under both of the BH and PH scenarios over the simulation, and the index reached 0.21 and 0.24 at the end of simulation, respectively (Figure 7). In comparison with the BH scenario, the PH scenario averagely increased the Bray–Curtis dissimilarity index by 0.03 with a relative increase of 33.2% during the simulation period.

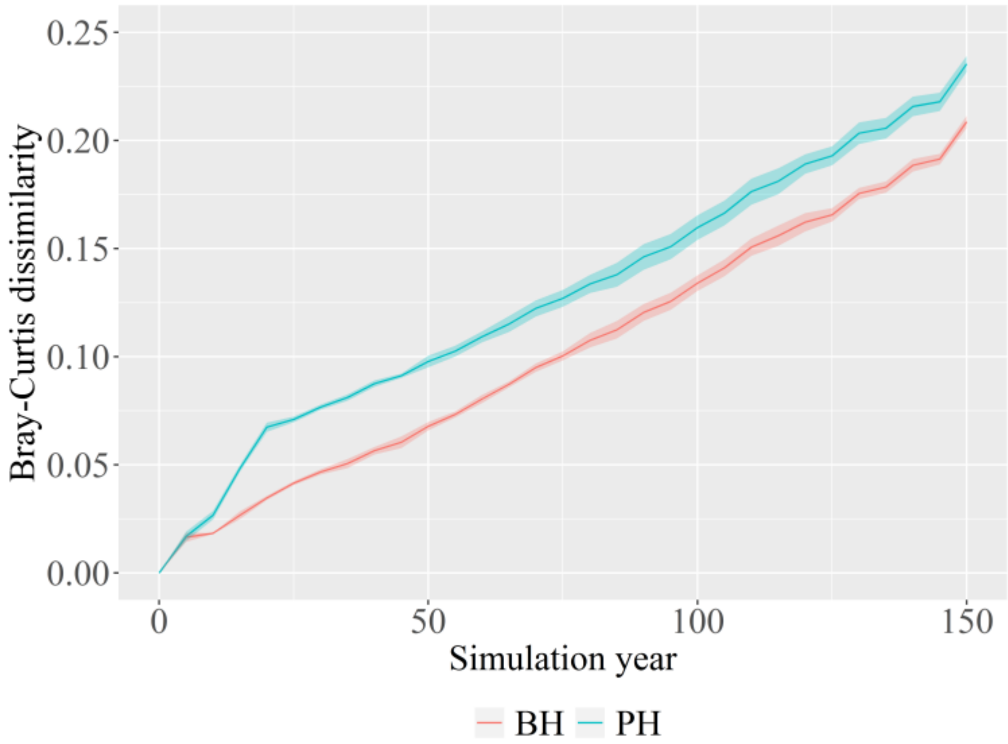

Figure 7. The Bray–Curtis dissimilarity index of species composition under the BH and PH scenarios over the simulation compared with the initial year. BH, the baseline scenario; PH, the historical PSH scenario. Error bands indicate one standard deviation of the five replicates.

The historical PSH significantly decreased the importance of Korean pine, while it remarkably increased spruce and fir in the disturbed forest. Compared with the BH scenario, the PH scenario decreased the importance value of Korean pine by 0.05 on average with a relative decrease of 12.2% (Figures 8a and 9a, $p < 0.01$) but increased both spruce and fir by 0.02 with relative increases of 5.1% and 6.0% (FIgures 8b,c and 9b,c, $p < 0.01$), respectively. The PH scenario barely increased the importance value of larix, ash, walnut, corktree, oak, elm, maple ($p < 0.05$), ribbed birch ($p < 0.05$), dahur birch, linden, and white birch in comparison with the BH scenario, while little decreasing poplar, with a range from 0.001 to 0.003 and a relative change from 0.5% to 2.8% (Figures 8d–o and 9d–o).

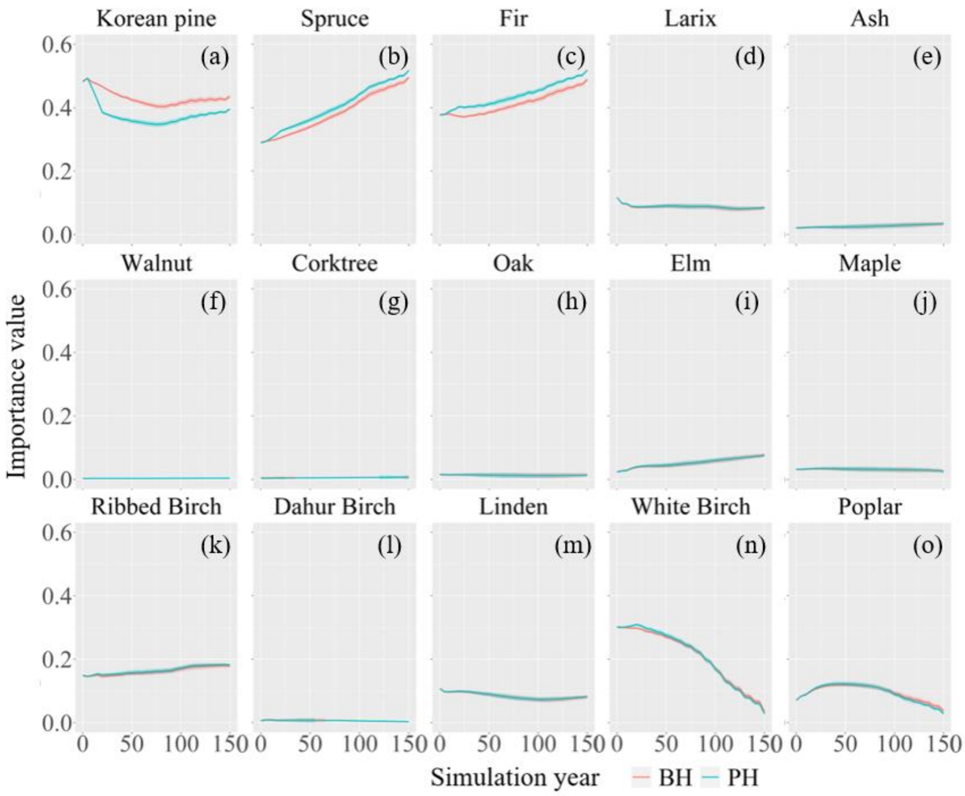

Figure 8. The importance value of each species during the simulation period under the BH and PH scenarios. BH, the baseline scenario; PH, the historical PSH scenario. Error bands indicate one standard deviation of the five replicates.

Figure 9. Relative changes in the importance value of each species under the PH scenario compared with the BH scenario over the simulation. Error bands indicate one standard deviation of the five replicates.

4. Discussion

The previous studies showed that seed harvesting decreased the quantities of seed bank and seedling bank at the site or stand scale [10–12], while it was unclear how such a disturbance affected the MKPBF at the landscape scale. We applied a forest landscape model to quantify the legacy effect of seed harvesting on the mixed Korean pine and broadleaf forest (MKPBF) at the landscape scale, which broadened understanding of seed harvesting at the large temporal and spatial scales. Seed harvesting, a spatially landscape process, can occur to a large spatial extent, such as several to hundreds of hectares, which not only affects the disturbed landscape, but also has impacts on the landscape adjacent to the disturbed landscape by seed dispersal. Seed harvesting directly reduces provenance and also indirectly synergizes with the stand-scale competition to limit the effectiveness of seed dispersal in these direct or indirect ways, which further adversely affects the regeneration and recovery of target tree species. A recent study found that the provenance restriction of Korean pine decreased the effectiveness of seed dispersal and impeded the Korean pine recruitment and the recovery of secondary forests to the MKPBF [14], which was consistent with our result.

Our result showed that the historical predatory seed harvesting (PSH) unremarkably altered the age structure of Korean pine throughout the simulation. Compared with the baseline scenario, although the historical PSH insignificantly decreased the age structure diversity of Korean pine during the whole simulation period, it resulted in a decreasing trend of diversity in the medium- and long terms (Figure 3). However, if the PSH continued for a long time, it would evidently reduce the age structure diversity of Korean pine in the long run. A previous study found that such high seed harvesting significantly decreased the distribution of the Korean pine young age cohort [4], which was consistent with our result. In addition, we found that the adverse effect of the historical PSH on young Korean pine had a significant cascade effect and lessened the abundance of older age cohorts (Figure 3).

The legacy effects of the historical PSH are long lasting, and the differences in tree species composition and succession trajectory in future forests have mainly been caused by the PSH in the past 20 years. Our result showed that the historical PSH remarkably decreased the dominance of Korean pine while significantly increasing spruce and fir (Figures 5 and 6). This is due to the fact that the PSH reduces the provenance of Korean pine and decreases its chances of colonizing and establishing, which further releases the growth space that would otherwise be occupied by Korean pine. Spruce and fir seedlings occupy the released growth space since they are the climax species in the mixed Korean pine and broadleaf forest region and they share similar ecological niches to Korean pine [29], which thus contributes to their dominance. Our result found that the succession trajectory of the disturbed forest landscape was significantly different, and the trajectory was altered from that dominated by the MKPBF to that dominated by the spruce, fir and broadleaf forest (Figures 7–9). The previous study based on the gap model found that the abundance of Korean pine significantly decreased with the reduction of saplings [30]. We infer that once the PSH lasts for a long time, it will be bound to change the succession trajectory of the MKPBF to a greater extent. However, a previous study based on the gap model found that the MKPBF would eventually evolve into a mixed broadleaved forest in the absence of Korean pine provenance [16], which is inconsistent with our result. This is because the initial stand condition in their sampling sites excludes species such as spruce and fir that occupied similar ecological niches to Korean pine, and because the gap model can only simulate forest succession at the stand scale but cannot spatially simulate seed dispersal. However, the forest landscape model is used to consider more tree species and seed dispersal process at the landscape level in this study, which can more truly reflect the forest succession dynamics.

The PSH has become an important obstacle to the regeneration and restoration of the MKPBF. The previous studies found that seed predation and seedling damage by terrestrial small mammals were often primary limitations that adversely influenced the regeneration and community dynamic of the coniferous forest, particularly in the case of an insufficient seed supply due to excessive human seed harvesting [10,31,32]. Korean pine relies on the rodents with a propensity to bury food to finish seed dispersal, and they are both predators and dispersers. When seeds are in short supply, the rodents prefer to eat them in situ rather than spread and bury them [32]. Due to the historically excessive timber harvesting of Korean pine and the continued PSH, the stock of Korean pine seed in the secondary forest is difficult to meet the consumption levels by predators, and therefore, few Korean pine seeds escape predation and successfully germinate, which seriously hinders the regeneration of Korean pine [14]. Thus, the intensity and rotation of seed harvesting should be severely restricted in the future to ensure that there are enough seeds to sustain the regeneration of Korean pine and the recovery of the MKPBF.

Future forest management should also focus on how to promote the restoration of the MKPBF through artificial silvicultural treatments, such as direct seeding or seedling planting so as to ensure the sustainable management of the MKPBF. A recent study found that only 9% of Korean pine seedlings survived after direct seeding due to large amount of animal feeding, while seedlings planting in forest gaps had a higher survival proportion, which was a more effective method to promote the regeneration of Korean pine and the recovery of the MKPBF [32]. However, planting seedlings is costly, and the costs connected with seedling plantation (such as transportation, planting, weeding, watering, and long-period management) might significantly restrict the potential application of seedling plantation over the large spatial extent. Additionally, the planted seedlings might initially have insufficient resistance to cope with extreme natural or anthropogenic disturbances. In comparison with planting seedling, direct seeding is a simple and cheap treatment [33,34]; although the survival ratio of seedlings is not high, it can also promote tree regeneration to a certain extent [35]. Therefore, direct seeding might be more appropriate for restoring the MKPBF within a large spatial extent.

Our study also had some limitations. Ignoring that the population dynamics of animals that feed on Korean pine seeds might increase uncertainty about the impact of seed harvesting on the regeneration of Korean pine, generally, Korean pine mainly depends on the seeds buried by animals to complete regeneration [32]. However, seed harvesting would reduce the food source of these animals, which would decrease their population and might subsequently reduce the magnitude of buried seeds, and therefore adversely affect the regeneration of Korean pine. We assumed that the boundaries of the current management area and stand remained consistent throughout the simulation, but forest management policies might adjust in the future, and changes in policies might alter these boundaries. Although these neglected factors might increase the uncertainty of the model prediction, our results still reflect the legacy effects of the historical PSH on the composition and structure of the MKPBF in the future and provide a reference for the restoration of the MKPBF at the landscape scale.

5. Conclusions

We demonstrated how to quantify the effects of seed harvesting at the landscape scale by a forest landscape model, LANDIS PRO, in this study. We evaluated the legacy effects of the historical predatory seed harvesting (PSH) on species composition and structure of the mixed Korean pine and broadleaf forest (MKPBF) for 150 years in the future. We found that the historical PSH had a cascading effect on the age structure of Korean pine, and the adverse effect was transmitted from the young cohort to the older cohort. Although the historical PSH had negative effects on all age cohorts of Korean pine, it altered insignificantly the diversity of the age cohort of Korean pine. The historical PSH had a long-lasting effect and would decrease the dominance of Korean pine but increase spruce and fir. Additionally, we found that the historical PSH would change the succession trajectories of the disturbed stand and would transform the succession pattern from Korean pine as the predominant species to spruce and fir. Future forest management should reduce the intensity and rotation of seed harvesting and consider using direct seeding or seedling planting to promote the recovery and sustainable development of the MKPBF.

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