Wang et al. Ecological Processes (2022) 11:1
https://doi.org/10.1186/s13717-021-00352-y

Ecological Processes

RESEARCH

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Cascading effect of source limitation on the granivore-mediated seed dispersal of Korean pine (*Pinus koraiensis*) in secondary forest ecosystems

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Abstract

Background: Granivore-mediated seed dispersal is susceptible to changes in seed availability and silvicultural management, which alters synzoochorous interactions in the antagonism-mutualism continuum and affects the seed dispersal effectiveness (SDE), and eventually, the plant recruitment. We conducted a whole-year study of seed addition to quantify the granivores-Korean pine (*Pinus koraiensis*) synzoochorous interactions and the SDE in the same secondary forests with two treatments. Both treatments had seed source limitations: one was caused by the disappearance of Korean pine due to the historical disturbance, the other by pinecone harvesting in Korean pine plantations adjacent to the secondary forests. Thinning with different intensities (control, 25%, and 50%) were also performed to further explore the synzoochorous interactions and SDE in response to silvicultural management in the second type of forests.

Results: Source limitation increased the proportion of pre- and post-dispersal seed predation, and made the granivores-Korean pine interaction shift more towards antagonism, with the estimated SDE of 2.31 and 3.60, respectively, for the secondary forests without and with Korean pine. Thinning with different intensities did not alleviate the reactions towards antagonism but altered SDE; granivores occurrence decreased, but the proportion of pre- and post-dispersal seed predation increased, resulting in a fivefold decreased seedling recruitment in 25% thinning (the lowest SDE of 0.26).

Conclusion: The source limitation coupling thinning biased the synzoochorous interactions more towards antagonism and significantly lowered granivore-mediated SDE, which limited the successful recruitment of Korean pine in secondary forests. Forest managers should control pinecone harvesting, protect the synzoochorous interaction, and take into account masting event for Korean pine regeneration in the future.

Keywords: Human disturbance, Thinning treatment, Synzoochorous interaction, Forest restoration

Introduction

In many forest ecosystems, granivore-mediated seed dispersal is essential to the natural regeneration of their dominant nut-bearing species, and ultimately influences plant community composition and structure (Boone and Mortelliti 2019; Gomez et al. 2019). These granivorous animals often play a dual role, simultaneously as an effective seed disperser and as a seed predator, which

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is defined as synzoochory (Zong et al. 2010; Bogdziewicz et al. 2020). As seed dispersers, they regularly drop and hoard seeds during transport, and fail to recover or incompletely consume all the cached seeds, resulting in seed germination in the cached site (Vander Wall and Longland 2004; Pesendorfer et al. 2016). As seed predators, they frequently consume a proportion of either pre-dispersed seeds (Nuñez et al. 2008; Zong et al. 2010; Xu et al. 2015) or post-dispersed seeds (Heggenstaller et al. 2006; Maron et al. 2012). Therefore, synzoochorous interactions are not exclusively antagonistic or mutualistic (Gomez et al. 2019; Bogdziewicz et al. 2020). Natural or human-induced changes often alter the availability of suitable seeds (Ruano et al. 2015; Peters and Visscher 2019), result in habitat loss or fragmentation for granivores (Chen et al. 2019; Zeng et al. 2019), and further influence the synzoochorous interactions. Together, synzoochorous interactions and environmental conditions determine the seed dispersal effectiveness (SDE), and eventually, affect the plant recruitment in the landscape (Schupp et al. 2010; Charco et al. 2017; Sawaya et al. 2018; Jácome-Flores 2019).

For those species depending on synzoochorous interactions, seed availability limitation may trigger a series of cascading effects. Previous studies reported that poor seed dispersal could be caused by excessive pre-dispersal seed predation or insufficient abundance of granivores (McKinney and Fiedler 2010; Xu et al. 2015; Čepelka et al. 2020). Furthermore, fewer deposited seeds escape consumption and survive in the winter safely (particularly for dormant seeds) due to high proportion of post-dispersal seed predation (Maron et al. 2012; Morán-López et al. 2016; Zwolak et al. 2016; Turley et al. 2017). Consequently, lower proportion of seedlings survives due to a high proportion of rodent excision in the stage of seed germination, which has been reported in many species such as oaks (*Quercus variabilis*, *Q. rubra*, *Q. palustris)* and black spruce (Côté et al. 2003; Shi et al. 2018; Yi et al. 2019). Although these phenomena are clearly described in the literature (Acácio et al. 2007; Piao et al. 2011), few researches integrate the cascading effects triggered by seed limitation for the whole phase of seed-to-seedling transition of dominant tree species.

Seed harvesting is one of the human-induced disturbances on seed availability (Piao et al. 2011; de Oliveira Wadt et al. 2018). Humans, motivated by economic interests, directly compete with animals for edible seeds. For example, humans harvest over 85% of Korean pine (*Pinus koraiensis*) seeds in Changbai Mountains (Piao et al. 2011), and Brazil nuts (*Bertholletia excelsa*) harvest can bring an income of US $166 million/year in Bolivia, Brazil, and Peru (de Oliveira Wadt et al. 2018). However, there is a divergent effect of source limitation on synzoochorous interactions and granivore-mediated seed dispersal effectiveness. For instance, there is poor recruitment of Korean pine after seed harvesting (Liu et al. 2004; Piao et al. 2011), but almost 8% of remaining Brazil nut seeds after harvest are enough for its recruitment in South America (de Oliveira Wadt et al. 2018). Therefore, it is necessary to explore how the source limitation affects synzoochorous interactions and granivore-mediated SDE.

A series of silvicultural treatments (e.g., thinning, forming forest gaps) has been proved to affect granivore-mediated seed regeneration (Ruano et al. 2015; Sun et al. 2016; Wang et al. 2019). Compared with control, thinning treatment can provide a niche with sufficient light environment for understory, alter food and shelter for granivorous animals, either increasing the risk of post-dispersal seed predation (Caccia et al. 2009; Dracup et al. 2015; Yu et al. 2017) or increasing the quantity and survival of cached seeds (Wang et al. 2019), subsequently affect the regeneration of dominant tree species (Tardós et al. 2019). However, there is little information available regarding that how the thinning treatment affects synzoochorous interactions and granivore-mediated SDE under the circumstance of seed limitation.

Mixed broadleaved and Korean pine forests are the primary forests in Northeast China and the Far East region of Russia (Miyaki 1987; Zhang et al. 2013). However, after decades of destructive timber exploitation and a large fire in the early 1950s, the primary forests were degraded into secondary forests with the lack of Korean pine, and secondary forests have become the major forest resource (accounting for more than 70%) in Northeast China (Zhu et al. 2007; Yan et al. 2013; Zhang et al. 2013). Although a small area of Korean pine plantation (3.1×10^5 ha) has been established within the forest landscape dominated by secondary forests (National Forestry and Grassland Administration 2019), the poor recruitment of Korean pine persists in secondary forests, which threatens the restoration of mixed broadleaved and Korean pine forests (Zhang et al. 2013; Sun et al. 2016; Song et al. 2018). Korean pine can naturally recruit depending on only seed regeneration (including seed dispersal, soil seed bank, seedling establishment, etc.). Furthermore, once ripened and fallen from a tree, the nutrient- and energy-rich seeds of Korean pine within the cone must need the help of seed-dispersing granivores such as Eurasian red squirrel (*Sciurus vulgaris*) and spotted nutcracker (*Nucifraga caryocatactes*) (Lu 2003). After seed dispersal of Korean pine, it is only possible to realize its seed regeneration. However, the mechanisms of natural regeneration obstacle of Korean pine in secondary forests are still unclear.

This study aims to elucidate the regeneration obstacle mechanism of Korean pine and promote its seed regeneration in secondary forests. We focused on two questions: (1) how does the source limitation of Korean pine affect the granivore-mediated seed dispersal, especially for synzoochorous interactions and SDE? (2) Is it feasible to change the above synzoochorous interactions and granivore-mediated SDE with thinning treatment in secondary forests? Consequently, the same secondary forests with two treatments were selected in the present study, i.e., the secondary forests without Korean pine (historical disturbance caused the disappearance of Korean pine), and the same secondary forests with thinning treatment and Korean pine plantations distributed nearby with pine seeds being harvested. We hypothesized:

H1 The limitation of seed availability decreases the frequency of granivores activities, increases both pre- and post-dispersal seed predation, and decreases seed germination in the next spring, especially in the secondary forests where historical disturbances eliminated Korean pine.

H2 Thinning treatment changes the microhabitat conditions for granivores activity and promotes seed survival, weakens the above reactions to seed limitation, and is conducive for seed germination.

H3 Seed limitation causes a negative deviation for synzoochorous interactions and reduces the SDE, while thinning treatment improves SDE.

Methods

Study area and Korean pine

The study site is located in the temperate secondary forests in Qingyuan Forest CERN, Northeast China, which is located in Changbai Mountain (41°55′27″ N, 124°58′52″ E, and 500–1100 m above sea level). The climate is a continental type with monsoon and windy spring, a warm and humid summer, and dry and cold winter. The annual average precipitation in the area is 810.9 mm, and the mean annual air temperature is 4.7 °C, with a monthly mean maximum of 22.11 °C in August and a monthly mean minimum of − 12.38 °C in January. The frost-free period lasts 130 days, and the growing season ranges from early April to late September (Zhu et al. 2007). The soil type is characterized as brown forest soil (brown forest soil containing 25.6% sand, 51.2% silt, and 23.2% clay) that is 60–80 cm thick (Yang et al. 2010; Lu et al. 2018). The secondary forests in Qingyuan Forest CERN are currently dominated by broadleaved tree species such as *Fraxinus mandshurica, F. rhynchophylla, Phellodendron amurense, Acer mono,* and *Quercus mongolica*. Only a small part of the secondary forests are surrounded by Korean pine plantations, leaving most of the secondary forests without the supply of Korean pine seeds in our study area (Fig. 1).

The cone of Korean pine (*P. koraiensis*) is large, with 10–17 cm in length and 252 ± 60.4 g in weight; each cone contains 70–184 viable seeds (Hayashida 1989). The flowering period is in June, and cone maturity is in September of the next year. Granivore-mediated Korean pine seed dispersal typically occurs in September. *P. koraiensis* is characterized by an obvious masting pattern, with an average mast interval of 3–5 years.

Study design

In total, 12 plots were chosen in the secondary forests without Korean pine plantations, and nine plots were selected in the secondary forests nearby Korean pine plantations (Fig. 1). Uniform thinning (control, 25%, and 50%; three plots for each treatment) was conducted in the secondary forests nearby Korean pine plantations in 2017. All of these plots were similar in topography (18–28° in slope, 158–228° in aspect, and mid-slope position), species composition, and tree size (the diameter at breast height (DBH) ranged from 20 to 35 cm). The tree densities in the control, 25% thinning, and 50% thinning stand were 608, 473, and 305 stems ha^{-1}, respectively. We set up one seed station per plot in the secondary forests without Korean pine plantations (total 12 stations), and three stations per plot in the secondary forests adjacent to the Korean pine plantations (each station was set at a 12-m interval per plot, total 27 stations) (Fig. 1).

Quantifying granivores abundance

The infrared digital cameras (Ereagel Trail Cameras E1 series, Shenzhen, China) were locked to the ground and faced north or south in each seed station from the year 2018 to 2019. We set the camera to take three photos after each trigger in each seed station (a total of 27 cameras), and the time interval between each trigger was 10s. All cameras were operated 24 h a day. We downloaded photos and checked batteries every 2-3 months; identified the animal types and the occurrence frequency by Image Information Management System (IIMS) (Murphy et al. 2017).

Seed releasing and tracking

Korean pine seeds were collected from cone-pickers and floated in water to exclude insect-damaged/empty seeds (Jansen et al. 2014). A 0.3-mm-diameter hole was created in each experimental seed through a drill, and a unique ID plastic tag (3 cm × 2 cm) with a 12-cm thin steel thread was individually attached in the hole of seed (Xiao

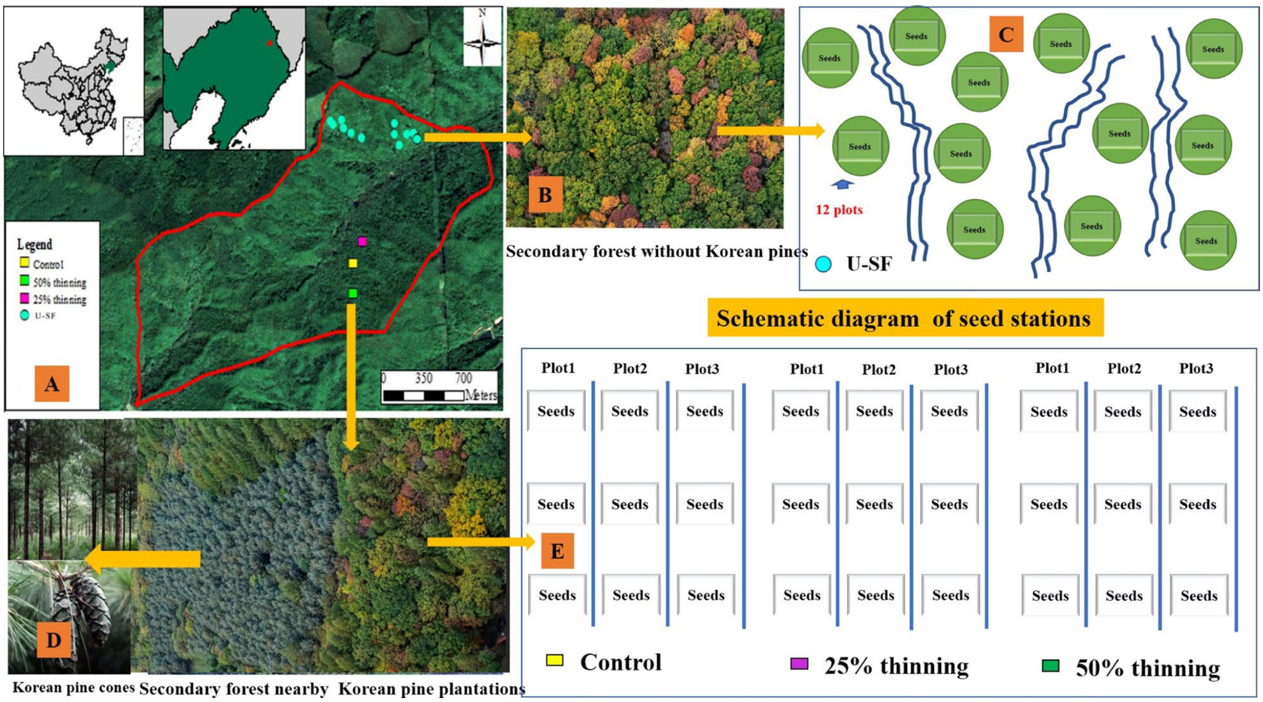

Fig. 1 Spatial distribution of the same secondary forests with two treatments (**B**, **D**) in the study area (**A**), and schematic diagram for the location of seed stations in stands (**C**, **E**). U-SF: secondary forests without Korea pine plantations

et al. 2013; Xiao and Zhang 2016). We evenly placed 200 tagged seeds at each seed station for 12 times, from the early autumn (late August) of 2018 to the summer (July) of 2019 (total of 2400 seeds at each seed station). Following the seed predation, removal and cache by granivores, we recorded seed fates by searching the plastic tags with ID leaving outside. The seed fates recorded included: pre-dispersal seed predation (Pre-DSP), post-dispersal seed predation (Post-DSP), and scatter-hoarding seed escaped predation (SH-EP). The recording was made every day in the first 3 days of seed release, and then we tracked seed fates every other day in the later period until all of the seeds were removed or consumed from the seed station.

Seedling emergence, survival and growth in the field

When the tagged seeds were dispersed and cached by granivores, untagged healthy seeds were cached at similar depths nearby labeled seeds (the tagged seed cannot germinate with damaged embryo). These untagged seeds were monitored for seedling emergence, survival, and growth in June–September 2019. We investigated the amount of 1-year Korean pine seedlings every month in each seed cached site. We tagged each seedling found and recorded its coordinates. We also assessed the light environment (Canopy openness) of individual seedlings using hemispherical "fisheye" photography. Photographs were taken with Canon 6D and Canon 8–15 mm f/4L USM hemispherical lens. Images were processed by the Gap Light Analyzer Software (Sun et al. 2016; Xie et al. 2020). The relevant results are shown in Additional file 1: Fig. S1.

Data analysis

The mutualism–antagonism continuum of synzoochorous interactions were operationally defined as the proportion of scatter-hoarding seed escaped predation (positive effects) minus the proportion of both pre-dispersal and post-dispersal seed predation (negative effects) (Gomez et al. 2019). Seed dispersal effectiveness (SDE) was calculated as the number of seeds dispersed by dispersal agents multiplied by the probability that a viable dispersed seed will survive, germinate, and produce a new seedling (Schupp et al. 2010).

To test Hypothesis 1: the cascade effect of source limitation on granivore-mediated seed dispersal, we performed generalized linear mixed models (GLMMs) to identify the difference of granivores activities, the amount of pre-dispersal seed predation, post-dispersal seed predation, scatter-hoarding seed escaped predation and germinated seedlings (survival or excised by granviores) in secondary forests with or without Korean pine. We applied GLMMs with negative binomial error distributions for granivore occurrence data with non-normally distributed and over-dispersal, and GLMMs with binomial error distributions followed by Wald's χ^2 test for other data. We took forest type (with and without Korean pine), season, and their interaction as fixed factors, and the provisioning station nested in the plot as a random effect to control for both repeated sampling and non-independence in the secondary forest.

To test Hypothesis 2: the effect of thinning treatment with different intensities, we replaced the "forest type (with and without Korean pine)" as "thinning treatment" in above fixed factor, and performed GLMMs again with others unchanged. All analyses were performed with the glmmTMB package in R software (Brooks et al. 2017).

To test Hypothesis 3: the effect of source limitation and thinning on synzoochorous interactions and SDE, an independent-samples *T*-test was used to examine the effect of source limitation on the outcome of mutualism–antagonism synzoochorous interactions and SDE (performed with MASS package in R language). One-way ANOVAs, followed by Tukey's post hoc tests, were conducted to examine the effects of thinning treatment with different intensities on synzoochorous interactions and SDE (performed with multcomp package in R software).

Results

Effects of source limitation on granivore activities and seed fates

The significant difference in granivores occurrence was shown between the two treatments for secondary forests. The frequency of granivores occurrence was 60% higher in the secondary forests without Korean pine plantations, especially for *S. vulgaris* and *N. caryocatactes* (Table 1; Additional file 1: Table S2). However, except for *N. caryocatactes* and *T. sibiricus*, granivores occurrence displayed no significant seasonal variation (Table 1; Fig. 2); a higher occurrence of *T. sibiricus* was shown in summer and autumn, *N. caryocatactes*, vice versa (Additional file 1: Table S1; Fig. 2).

Pre-dispersal seed predation was 57.0% and 67.0%, while post-dispersal seed predation was 19.3% and 11.5%, in the secondary forests without and with pine plantations, and the differences were significant (Table 1; Fig. 3). About 1.9% and 3.1% of seeds were escaped from predation and cached intact, in the secondary forests without and with pine plantations, respectively, but the difference was not significant (Additional file 1: Table S3, Fig. 4). Among those seeds cached intact, a few seeds escaped the predation and germinated, resulting in a 0.7% and 1.1% seed germination rate in the secondary forests without and with Korean pine plantations, respectively. Among those germinated, granivores excised 34.4% and 28.4% seedlings in the secondary forests without and with Korean pine plantations, respectively (Table 1; Additional file 1: Table S3; Fig. 4).

The occurrence of granivores

After the whole year's infrared camera monitoring, the main types of animals were *S. vulgaris*, *N. caryocatactes*, *Tamias sibiricus*, *Apodemus peninsulae*, *Mesechinus hughi*, *Lepus mandshuricus*, *Mustela sibirica*, *Meles meles*, and *Accipiter gentilis* (Additional file 1: Fig. S2). Among these animals, *S. vulgaris*, *N. caryocatactes*, *T. sibiricus*, and *A. peninsulae* belong to granivores

Table 1 Effects of source limitation due to historical disturbance and human competing with pinecones, thinning treatments and season on granivores activities and Korean pine seed regeneration processes

Fixed effect	Source limitation			Season			Thinning treatments			Season		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Animal occurrence	6.36	1	**0.01**	5.29	3	0.15	11.71	2	**0.01**	13.64	3	**0.02**
Sciurus vulgaris	5.86	1	**0.02**	5.80	3	0.12	8.30	2	**0.02**	5.06	3	0.17
Tamias sibiricus	0.08	1	0.78	22.67	3	**0.00**	5.80	2	**0.05**	16.47	3	**0.01**
Nucifraga caryocatactes	9.48	1	**0.00**	47.73	3	**0.00**	2.29	2	0.32	12.77	3	**0.00**
Apodemus peninsulae	1.37	1	0.24	6.42	3	0.09	3.30	2	0.16	16.20	3	**0.00**
Seed regeneration processes												
Pre-dispersal seed predation	9.68	1	**0.00**	20.68	3	**0.00**	3.88	2	0.14	5.13	3	0.16
Post-dispersal seed predation	1.21	1	0.27	41.41	3	**0.00**	10.006	2	**0.01**	128.48	3	**0.00**
Scatter-hoarding seed escaped predation	23.64	1	**0.00**	7.09	3	0.07	1.87	2	0.39	64.51	3	**0.00**
Seedling recruitment	6.30	1	**0.01**				116.32	2	**0.00**			
Seedling survival	0.01	1	0.97				4.24	2	0.12			
Seedling mortality	0.01	1	0.98				12.80	2	**0.00**			

Significant effects ($P < 0.05$) are bolded

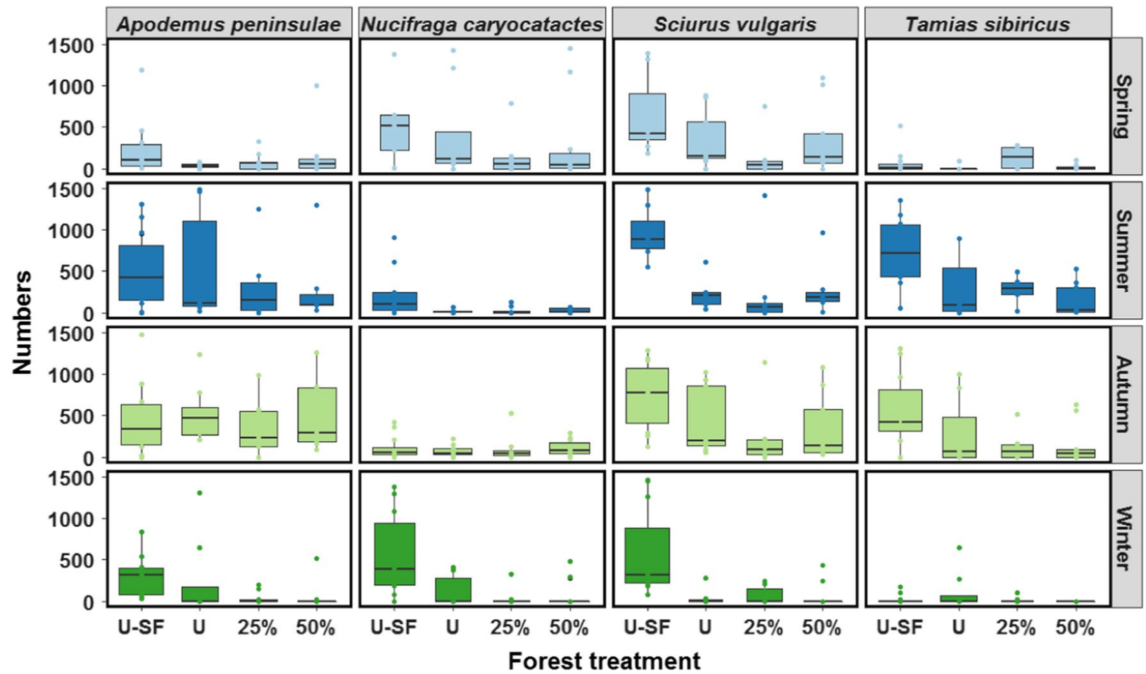

Fig. 2 Granivore occurrence in secondary forests. U-SF: secondary forests without Korea pine plantations; U: secondary forests adjacent to Korea pine plantations. 25%: 25% thinning treatment; 50%: 50% thinning treatment

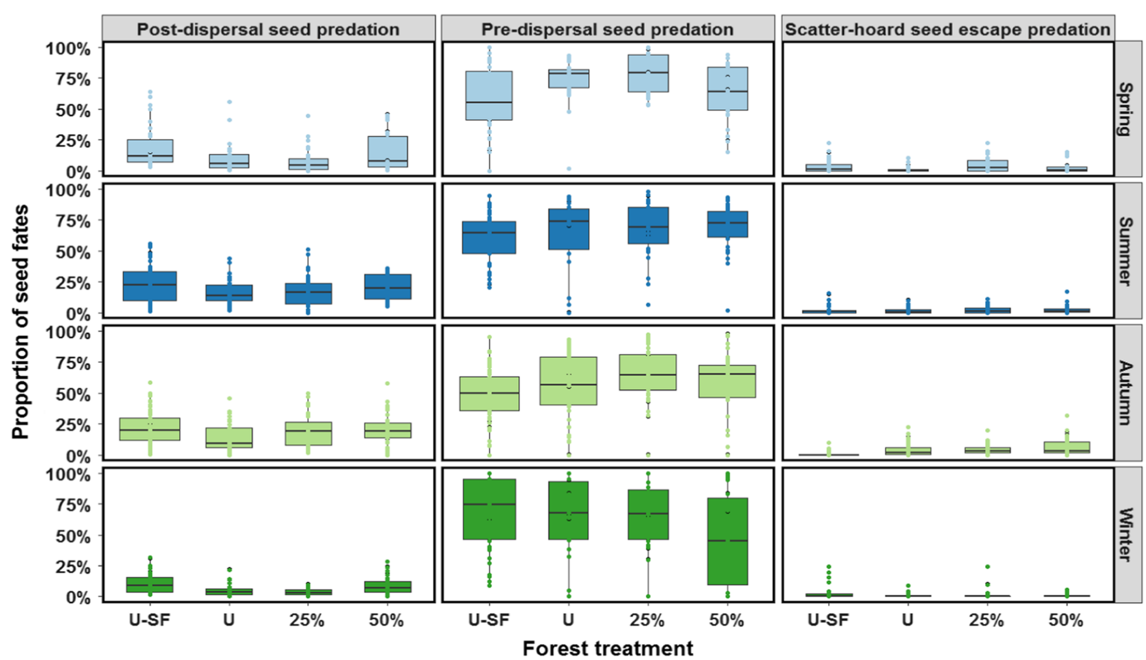

Fig. 3 The proportion of pre-dispersal seed predation, post-dispersal seed predation, and scatter-hoarding seed escaped predation in the secondary forests. U-SF: secondary forests without Korea pine plantations; U: secondary forests adjacent to Korea pine plantations. 25%: 25% thinning treatment; 50%: 50% thinning treatment

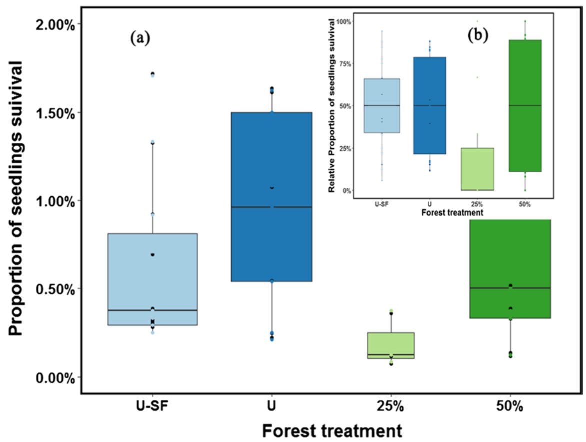

Fig. 4 The proportion of total seedling recruitment (**a**), and the relative proportion of seedling survival (**b**) in the secondary forests. U-SF: secondary forests without Korea pine plantations; U: secondary forests adjacent to Korea pine plantations; 25%: 25% thinning treatment; 50%: 50% thinning treatment

and regularly appeared in every plot, others occasionally appeared (Additional file 1: Table S1). The animal with the highest frequency was *S. vulgaris*, followed by *Nucifraga caryocatactes* and then by *T. sibiricus*, all of which are both seed dispersers and seed predators (Fig. 2; Additional file 1: Fig. S2). *A. peninsulae* and *M. hughi* are pure seed predators, while *Accipiter gentilis* is the predator of *S.* vulgaris (Additional file 1: Fig. S2).

Effects of thinning treatment on granivores activities and seed fates

Thinning and season significantly affected the occurrence of granivores (Table 1). The rank of granivores occurrence was as follows: control > 50% thinning > 25% thinning, and summer > autumn > spring > winter (Fig. 2). Among animals, the frequency was *S. vulgaris* > *A. peninsulae* > *N. caryocatactes* > *T. sibiricus* (Fig. 2). There was a significant interaction between animal type and season (F=40.54, df=9, P<0.001). Thinning significantly affected *S. vulgaris*, which occurred significantly less in 25% thinning stands than in control, but the season did not (Table 1; Additional file 1: Table S4; Fig. 2). *N. caryocatactes* was not affected by thinning, but it was affected by season, i.e., summer > winter > spring > autumn (Table 1; Additional file 1: Table S4; Fig. 2). *T. sibiricus* was affected by thinning, with control > 50% thinning > 25% thinning, and by season with summer > autumn » spring » winter (Table 1; Additional file 1: Table S4; Fig. 2). *A.* peninsulae was not affected by thinning, but it was affected by season with summer > autumn > spring » winter (Table 1; Additional file 1: Table S4; Fig. 2).

Although thinning and season did not significantly affect pre-dispersal seed predation, they did significantly affect post-dispersal seed predation (Table 1; Additional file 1: Table S5). No significant interactions were found between seasonal and thinning treatment for either pre-dispersal seed predation or post-dispersal seed predation. The proportion of post-dispersal seed predation was highest in 50% thinning treatment (averaged 16.5%, 12.5%, and 11.5% in 50% thinning, 25% thinning, and control stand, respectively). The post-dispersal seed predation in different seasons changed as follows: summer > autumn > spring > winter. The thinning treatment did not significantly affect the scatter-hoarding seeds that escape predation (Table 1; Additional file 1: Table S5; Fig. 3). Only 2.5–3% of seeds survived the winter regardless of treatment. However, there was a difference in the rate of scatter-hoarding seeds that escape predation in different seasons (Table 1; Additional file 1: Table S5). The highest rate of scatter-hoarding seeds that escape predation was shown in the autumn; the lowest was found in winter (on average, autumn was 5.3%, spring was 3%, summer was 2%, winter was 1%) (Fig. 3).

Thinning treatment had significantly negative effects on Korean pine seedling recruitment and mortality (Table 1). The result showed that the proportion of total germinated 1-year seedlings in control (1.1%) was higher than those in thinned stands, five-fold higher than 25% thinning treatment, and 1.7-fold higher than 50% thinning treatment (Fig. 4a). Among these seedlings, seedling mortality was higher in 25% thinning treatment (77.8%) than in control (24.8%), and the rest of 72.7%, 22.2%, and 85.2% seedling survived well in control, 25% and 50% thinning treatment (Table 1; Fig. 4b).

Synzoochorous interactions and granivore-mediated seed dispersal effectiveness

There was a significant difference in the mutualism–antagonism continuum of synzoochorous interactions between the two treatments for secondary forests (F = 2.21, df = 1, P = 0.04), but not among thinning treatments (F = 0.03, df = 3, P = 0.97) (Fig. 5a). The average outcome of positive effect minus negative effect was − 0.76 in the secondary forests without pine plantations, which is more biased to negative than in the secondary forests adjacent to Korean pine plantations (− 0.69). There was no significant difference in SDE between the two treatments for secondary forests (F = 1.27, df = 1, P = 0.27) (Fig. 5b), but a significant difference was observed among thinning treatments (F = 5.66, df = 3, P = 0.003) (Fig. 5c); the average outcome of SDE was 3.60 in control, 0.26 in 25% thinning treatment, and 2.90 in 50% thinning treatment.

Discussion

Cascading effects of source limitation on granivores activities, seed germination, and seedling survival

Historical disturbances, particularly logging, caused a significant decline of *Pinus koraiensis*, which degraded mixed broad-leaved Korean pine forests into secondary forests (Zhu et al. 2007; Yang et al. 2010). Therefore, Korean pine plantations were established to offer the seeds for pine seedling recruitment in secondary forests. Our results indicated that although protecting the seed source was necessary, pinecone harvesting persisted severely limited pine seedling recruitment, which was in line with the research of Piao (2011). Our results showed that almost 60% of seeds were consumed in situ, and 15% of seeds were eaten after dispersal (Fig. 3), which is much higher than the 22% predation of Korean pine seeds by Eurasian squirrels previously reported by Miyaki (1987). Our results further supported that, when seed scarcity had limited seed dispersal, granivores would be more inclined to eat seeds in situ than to disperse and cache seeds (Brocardo et al. 2018; Jácome-Flores et al. 2019). As a result, seeds would suffer heavy pre- and post-predation, especially for small and nutrient-rich pine seeds (Nuñez et al. 2008; Piao et al. 2011; Yu et al. 2014; Ruano et al. 2015).

Anthropogenic disturbances profoundly affected the seed dispersal process (Jácome-Flores et al. 2019). Some mammals changed their spatial distribution or activity patterns to avoid humans (Yang et al. 2018). We found that due to the lack of human disturbance caused by pinecone harvesting, the frequency occurrence of granivores was higher, but the proportion of pre-dispersal seed predation was lower in secondary forests without the Korean pine plantations than the secondary forests nearby Korean pine. However, due to food scarcity, the higher post-dispersal seed predation occurred in secondary forests without Korean pine plantations. Consequently, only 0.7% and 1.1% of seeds germinated successfully in secondary forests with/without Korean pine plantations, respectively. Among those successfully germinated seedlings, 28.4–34.4% seedling mortality was observed after the first growing season due to excision by rodents, fungal infection, and other unknown causes. The common situation of seedling excised by granivores has occurred in oaks or black spruce seedling in the food-scarce spring (Côté et al. 2003; Yi et al. 2019). However,

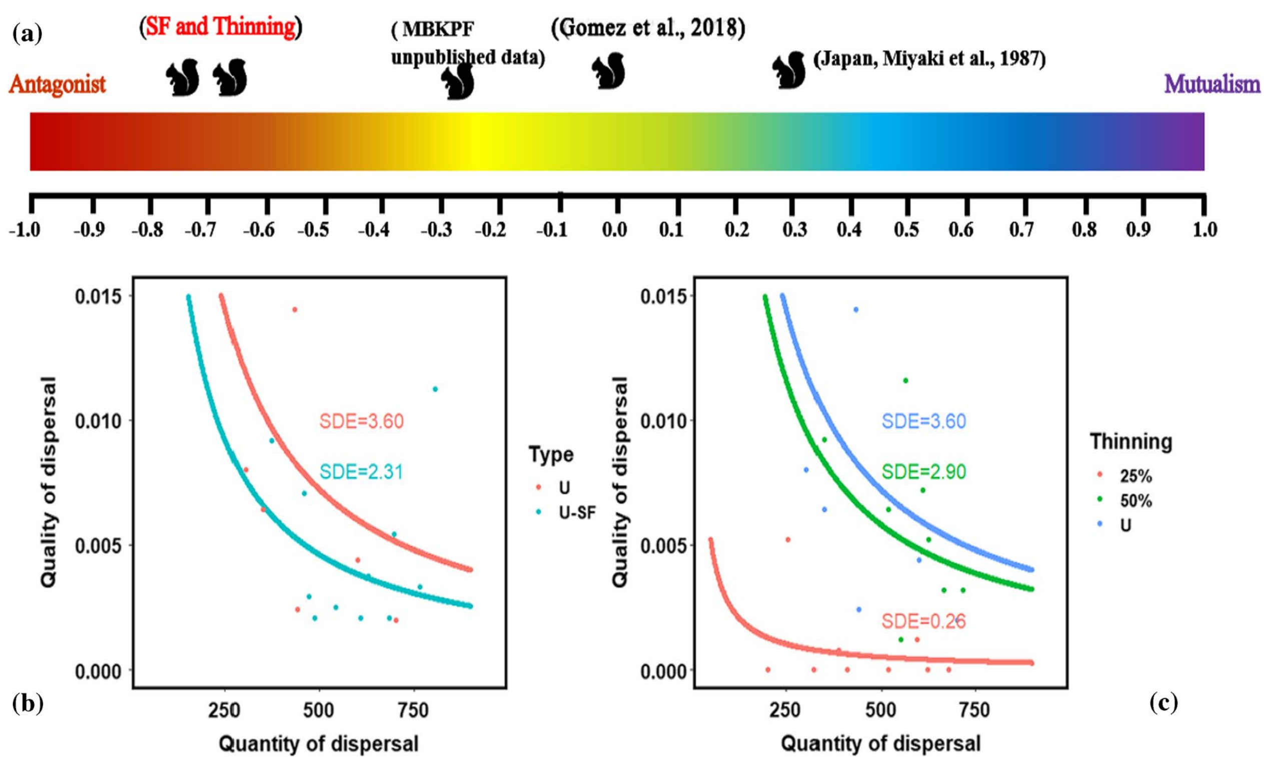

Fig. 5 The mutualism–antagonism continuum of synzoochorous interactions (**a**), granivore-mediated seed dispersal effectiveness in the same secondary forests with two treatments (**b**), and thinning treatment (**c**). SF: secondary forests; MBKPFs: mixed broad-leaved Korean pine forests; SDE: seed dispersal effectiveness; U-SF: secondary forests without Korea pine plantations; U: secondary forests adjacent to Korea pine plantations. 25%: 25% thinning treatment; 50%: 50% thinning treatment. The squirrels represented the mutualism–antagonism continuum of synzoochorous interactions of granivores

our research disagrees with the studies in South America, which suggested that harvesting pinecones did not result in seed exhaustion, and a small number of remaining seeds were enough for recruitment (de Oliveira Wadt et al. 2018). In our research, an average of less than 1.2% of seedling survival is difficult to maintain the regeneration and recruitment of Korean pine in the secondary forests.

Overall, our study supported Hypothesis 1 that the limitation of seed availability affects granivores' activities and decreases the survival of seeds, especially for those secondary forests without the Korean pine. The deficiency of seed source produced a cascading effect that ultimately prevented the recruitment of Korean pine and thus the restoration of secondary forests, which was in agreement with findings from others (Nuñez et al. 2008; Piao et al. 2011; Yu et al. 2014; Ruano et al. 2015).

Thinning treatment negatively affected granivore-mediated seed dispersal

Our results did not support Hypothesis 2 that thinning treatment affects granivore-mediated seed dispersal and promotes seed survival. Thinning negatively affected the granivore-mediated seed dispersal in secondary forests where pinecones were harvested in the adjacent plantations. We found that the animal activity frequency was less in the thinned stands (Fig. 2). The higher canopy openness resulted from thinning treatments likely discouraged animal occurrence, which supports previous studies that open habitats resulted in a lower granivore occurrence due to higher predation risk (Yu et al. 2017). We also found that the animal activity frequency was higher in summer and autumn, but lower in winter and spring, except for *N. caryocatactes*. This seasonal variation may be attributed to the quality and density of the interspecific synchrony or asynchrony of seed rain, with animals actively foraging during seed season (Ostoja et al. 2013; Xiao and Zhang 2016; Yang et al. 2020). However, the effect of thinning treatment on animal activity did not change with seasonal variation.

Our results suggested that lower foraging frequency did not reduce seed predation. The higher proportion of pre-dispersal seed predation and post-dispersal seed predation may be caused by that the desire for food counteracted the danger associated with the higher canopy openness in thinning treatment (Garcia-Del-Rey et al. 2009; Perea et al. 2011; Ziffer-Berger et al. 2017; Wang et al. 2019). A previous study reported that forest cover had a weak effect on seed predation when fruits were scarcer (Herrera et al. 2011). Compared with fruitful autumn, the increasingly higher proportion of pre-dispersal seed predation and post-dispersal seed predation occurred in the winter and spring of food shortages (Fig. 3). Thus, perceived predation risk, seed abundance and availability, and safe foraging options are all potentially affecting animal foraging (Garcia-Del-Rey et al. 2009). Although there is no obvious difference in the proportion of scatter-hoarding seeds that escape predation in thinning treatment, the final germinated seedlings in thinning stands were significantly lower than that in control, further proved the negative effect of thinning treatment on the granivore-mediated Korean pine seed dispersal and recruitment.

To some extent, our results indirectly supported a previous study that abiotic factors such as increased light level (created by thinning) may be unnecessary for the early regeneration of Korean pine (Zhang et al. 2013). We found the germinated seedlings were abundant under the 9–13% full sunlight observed in the control stand (Additional file 1: Fig. S1), and most of the secondary forests in our study area had >7% full sunlight to sustain the survival of seedlings (Sun et al. 2016). However, because of historical disturbance and persistent pinecone harvesting, few secondary forests have Korean pine seeds sufficient enough to satiate seed predators, allowing the cached seeds to escape predation and successfully germinate. Therefore, pinecone harvesting has become a significant obstacle to the recruitment of Korean pine (Kajimoto 2002; Piao et al. 2011).

Source limitation and thinning treatment changed the synzoochorous interactions and granivore-mediated seed dispersal effectiveness

The mutualism–antagonism continuum of synzoochorous interactions depends on both intrinsic (seed abundance, see Bogdziewicz et al. 2018; seed size, see Cao et al. 2016; seed chemistry, see Xiao et al. 2008, 2009) and extrinsic factors (competitors, see Gómez et al. 2019; the spatial structure of vegetation, see Aliyu et al. 2018; and landscape-scale disturbance, see Pesendorfer et al. 2016; Zeng et al. 2019). According to the results of Gómez (2019) and Miyaki (1987), the outcome of granivores–seed interactions fluctuates around zero in the context of abundant food. However, our results showed that due to seed source limitation resulting from pinecone harvesting, the average difference value indicated that the mutualism–antagonism continuum of synzoochorous interactions was more biased towards antagonism (Fig. 5a). In the mixed broad-leaved Korean pine forests with less human interference, we previously placed 100 seeds at each seed station and found that although fewer seeds added in seed station, the difference between the proportion of seed deposition and seed predation was significantly higher than those in the secondary forest found in this study (Fig. 5a; Additional file 1: Fig. S3). All of the evidence suggests that the human disturbance caused the negative deviation for mutualism–antagonism of synzoochorous interactions. The result is consistent with the part of hypothesis 3 that seed limitation results in a negative shift for synzoochorous interactions and reduces the seed dispersal effectiveness (SDE). Therefore, our results suggest that human-mediated disturbances may shift the positive effects of synzoochorous interactions to where interactions outcomes are detrimental for dispersal and regeneration (Jácome-Flores et al. 2019). Although the interactions between granivores and Korean pine seeds had a profound variation in the secondary forests with/without Korean pine, it did not impinge on the final SDE (Fig. 5b). Furthermore, thinning treatment did not significantly alleviate negative deviation for synzoochorous interactions, but decreased the SDE, especially in 25% thinning treatment (Fig. 5c). The reasonable explanation is that the mutualism–antagonism continuum of synzoochorous interactions may determine the quantity of dispersal (e.g., visitation frequency of animals, the amount of dispersed seeds), but maybe other abiotic factors affected the quality of dispersal (e.g., the probability of seed germination for dispersed seeds, the probability of seedling survival) (Schupp et al. 2010). Therefore, thinning treatment negatively affected granivore-mediated Korean pine SDE.

Study limitation

In this study, we selected two secondary forests to compare the effects of seed limitation (no seeds and few seeds) on synzoochorous interactions and SDE, one without Korean pine and the other nearby Korean pine plantations but with pinecones picking. Actually, secondary forests adjacent to Korean pine plantations without cone-picking should be used as the control for our study. However, such forests could not be found in the study area due to widespread pinecone harvest driven by economic profit. Therefore, we used published studies (Miyaki 1987; Hayashida 1989; Piao et al. 2011) and cross-regional field data to explain the findings of this study. Furthermore, the lack of replication is an unavoidable shortage in the design of this experiment. Due to the strict natural forest protection law in China, we were only permitted to conduct two thinning treatments with only one site per intensity level in secondary forests. As a result, we exercise caution in extrapolating the study results beyond the research sites.

Our study monitored the fates of dispersed seeds only for one year. A previous study indicated that only a small proportion of Korean pine seeds can germinate in the first spring after dispersal and the majority germinate in the second growing season after dispersal (Song et al. 2018), which suggests that the field data of seed germination with one-year survey could underestimate seed dispersal effectiveness. However, only less than 5% of the seeds survived after the first winter attribute to the higher proportion of granivore-mediated seed predation (Fig. 3). During this long period of ~ 20 months after dispersal, most of the seeds could be consumed by seed-caching granivores or deteriorated due to fungal attacks (Li et al. 2012; Lu et al. 2003). It is reasonable to believe that the remaining dormant seeds are almost impossible to survive the second winter at the cached sites. Therefore, we were convinced that the cascading effect of seed limitation directly caused the lower SDE. Apart from that, our results may underrate the amount of seed fates and germinated seedlings due to limited time and labor during the field investigation, depending on that the maximum dispersal distance is more than 4 km for *Nucifraga caryocatactes* and 1.8 km for *Sciurus vulgaris* (Lu et al. 2003). Thus, wider search range should be performed in the future study.

Although the field experiment was conducted in the non-mast year of Korean pine, this did not amplify the effect of the lack of food scarcity because these granivores aren't the forest specialist species and other alternative resources are also available to these predators, such as acorn (*Quercus mongolica*) and walnut (*Juglans mandshurica*) (Yang et al. 2016). However, given the SDE will be different between non-mast years and mast years (Li et al. 2017; Zwolak et al. 2016; Zhang et al. 2021), our studies should be run over more years in the future to illustrate that granivore-mediated Korean pine regeneration is inadequate to ensure the restoration of secondary forests into mixed broad-leaved Korean pine forests. Besides that, interspecific synchrony or asynchrony of seed rain plays a key role in the formation of animal-mediated seed dispersal (Yang et al. 2020; Yu et al. 2020), and seed rain compositions may further affect the dispersal success of Korean pine. For example, the presence of native oaks limits the dispersal of invasive ones in temperate Europe (Bogdziewicz et al. 2020) or enhances the dispersal of red oaks (Lichti et al. 2014). Therefore, the presence of other seeds complicates the issue of the influence of background pine seeds availability on dispersal, which should also be studied in the future.

Management implication

Synzoochorous interactions between the granivores and the Korean pine seeds determined the granivore-mediated seed dispersal effectiveness. Understanding where the synzoochorous interactions are located in the mutualism–antagonism continuum became essential to assess Korean pine recruitment and regeneration under the background of the human disturbance. Seed limitation had a cascading effect, decreasing the granivores' occurrence and seed dispersal, increasing pre-dispersal and post-dispersal seed predation and making the synzoochorous interactions shift more towards antagonism in the mutualism–antagonism continuum (predation effect becomes more dominant over dispersal effect). This cascading effect was more severe in the secondary forests, where historical disturbances eliminated Korean pine. Thinning did not enhance the granivore-mediated Korean pine seed dispersal effectiveness. It decreased granivores occurrence, but increased the proportion of pre-dispersal and post-dispersal seed predation, resulting in five-fold decreased in seedling recruitment under 25% thinning treatment. Lower granivore-mediated SDE led to poorer Korean pine recruitment in the secondary forest under the uncontrolled pinecone harvesting.

These results have implications for silvicultural practices that it is necessary to reduce the thinning treatment, control pinecone harvesting, and protect the synzoochorous interactions during the Korean pine seed regeneration in secondary forests. If not, artificial regeneration (e.g., direct seedings or planting seedlings) should be considered, which has been proved that planting seedlings is an effective way to implement the short-term successful recruitment of Korean pine in secondary forests (Wang et al. 2021). Further studies are still needed to be considered and performed in synchrony with a masting event in the future, benefiting from the satiation effect and the decreasing seedling grazed by herbivores.

Abbreviations

SDE: Seed dispersal effectiveness; Pre-DSP: Pre-dispersal seed predation; Post-DSP: Post-dispersal seed predation; SH-EP: Scatter-hoarding seed escaped predation.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-021-00352-y.

Additional file 1: Fig. S1 The canopy openness distribution of regenerated Korean pine seedlings. **Fig. S2** The main animals types shot by infrared camera. A: *Sciurus vulgaris,* B: *Nucifraga caryocatactes, C: Tamias sibiricus,* D: *Apodemus peninsulae,* E: *Mesechinus hughi,* F: *Lepus mandshuricus,* G: *Mustela sibirica,* H: *Meles meles*, I: *Accipiter gentilis* preying on *Sciurus vulgaris.* **Fig. S3** The proportion of Pre-DSP, Post-DSP and SH-EP in Changbai Mountain primary forests. Pre-DSP: Pre-dispersal seed predation, Post-DSP: Post-dispersal seed predation, SH-EP: Scatter-hoarding seed escaped predation. **Table S1.** The cumulative numbers of each type of animals recorded by infrared cameras during four seasons in different secondary forest treatments. U-SF: secondary forests without Korean pine plantations; U: secondary forests adjacent to Korea pine plantations. **Table S2.** GLMMs exploring the effects of seed source limitation due to historical disturbance and human competing with pinecones, and season on Korean pine-granivores activities. **Table S3** GLMMs exploring the effects of seed source limitation due to historical disturbance and human competing with pinecones, and season on Korean pine seed fates. Pre-DSP: Pre-dispersal seed predation, Post-DSP: Post-dispersal seed predation, SH-EP: Scatter-hoarding seed escaped predation. **Table S4.** GLMMs exploring the effects of thinning treatment and season on the main granivores occurrence. **Table S5.** GLMMs exploring the effects of thinning treatment and season on seed fates. Pre-DSP: Pre-dispersal seed predation, Post-DSP: Post-dispersal seed predation, SH-EP: Scatter-hoarding seed escaped predation.

Acknowledgements

The authors gratefully acknowledge the support from the China Scholarship Council. Many thanks to Junfeng Yuan, Ting Zhang, Jin Xie, for assisting in data collection.

Authors' contributions

JW, GGW, QLY and JJZ: conceived the ideas and designed the study. JW, RL, LZY and YRS: provided experiment equipment and collected field data. JW: analyzed the data and led the writing of the first draft of the manuscript. GGW, QLY and JJZ: substantially contributed to revising the manuscript. All authors contributed critically to the drafts and gave final approval for publication. All authors read and approved the final manuscript.

Funding

This work was financially supported by the National Natural Science Foundation of China (U1808201, 31830016), K. C. Wong Education Foundation (GJTD-2018-07), and Liaoning Revitalization Talents Program (XLYC1807102).

Availability of data and materials

Please contact the author for data requests.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 13 May 2021 Accepted: 6 December 2021
Published online: 04 January 2022

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