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Bringing the Natives Back: Identifying and Alleviating Establishment Limitations of Native Hardwood Species in a Conifer Plantation

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Abstract: To facilitate the reintroduction of five native late-successional Taiwanese Fagaceae species into Japanese cedar (*Cryptomeria japonica* (D.) Don) plantations, we experimented with methods to alleviate their establishment limitations. We tested different combinations of tree species, seedling development stages, and site preparation techniques. First, we directly sowed both fresh and germinated acorns under both closed and opened (thinned) canopies. Both fresh and germinated acorns survived only six months at most. Wildlife consumption was the most critical factor hindering their survival. We subsequently experimented with different methods for increasing establishment rates, such as thinning in combination with understory control, applying chemical animal repellents to seeds, using physical barriers against seed predators, and using seedlings of different ages. Among the methods experimented, none was effective. The effects of silvicultural treatments to deter seed consumption lasted only the first few weeks after sowing, whereas the effects of physical barriers were inconsistent. We also tested planting 3-month and 1-year-old seedlings. Seedling survival after 9 months was about 20% on average for 3-month-old seedlings but reached 80% for 1-year-old seedlings. Our results suggest that planting seedlings older than six months or establishing physical obstacles to prevent seed predation will be the most effective strategies to reintroduce late-successional hardwood Fagaceae species into Japanese cedar plantations.

Keywords: forest restoration; Fagaceae species; seed predation; seedling establishment; sub-tropical hardwoods; native mixed forests

1. Introduction

Forest biodiversity has been declining worldwide at an alarming rate over the past decades due to deforestation and forest fragmentation. Thus, developing effective strategies to restore forest biodiversity has been recognized as an essential element of biodiversity conservation [1]. It is suggested that plantation forests are excellent ecosystems for forest restoration, because of the microhabitat similarities between planted and natural forests [2]. Particularly, substituting planted monocultures with native mixed forests can also be a tool for increasing forest resilience to uncertain forest conditions [3]. Many plantation forests are no longer serving a timber production purpose, as in the case of Taiwan, where due to the rising awareness of conservation, management practices cannot be executed in conifer plantations, allowing natural succession to slowly take place [4]. Returning those plantation forests to their natural states provides a unique opportunity for forest restoration, and developing effective strategies to achieve that objective becomes an essential task for the conservation of forest biodiversity. Restoration guidelines for such a purpose, however, are not well established [2]. Given the unique ecological features of each plantation, and the lack of ecological knowledge on many non-commercial, subtropical native tree species, more empirical studies are required for establishing such guidelines.

Native hardwood species usually fail to return to plantation forests because of recruitment limitation (e.g., failure in seed dispersal, seed survival, or seedling survival). Planting nursery-grown seedlings and direct seeding are two common tools used to alleviate recruitment limitations of native species in forest restoration. The former has the advantage of a high success rate, but it also has the disadvantage of high costs. The latter has some biological benefits and the advantage of low cost, but its success rate is generally low [5–9]. Both approaches use plant materials that are thought to represent the most vulnerable stages during trees' life cycle [10,11].

Seed and seedling survival are limited by multiple biotic and abiotic factors [10,12,13]. Herbivory, light availability, and drought are the three most common and important causes of mortality [11]. Previous studies, however, have indicated that the relative importance of factors limiting seed and seedling establishment is highly context-dependent, and may vary among different ecosystems and sites [10]. Therefore, the success of restoration strategies depends on effectively identifying the critical stages of recruitment limitation. Thus, systematic empirical studies including seed and seedling stages are necessary to identify the critical stage of recruitment limitation.

Japanese cedar (*Cryptomeria japonica* (D.) Don, also known as *sugi*) plantations are a good case study for testing such empirical approaches. Introduced into Taiwan from Japan more than a century ago, Japanese cedar is the most widely planted tree species in Taiwan, covering approximately 1.1 percent (41,390 ha) of the island's total land area [4]. Due to the increasing production costs and declining timber prices, most of Taiwan's Japanese cedar plantations are either approaching or have passed the prescribed rotation age. Moreover, some existing Japanese cedar plantations were established on sites that are now considered unsuitable for timber production, primarily owing to concerns about watershed protection. To restore and promote biodiversity, the current local management plans mandate the restoration of these plantations by gradually reintroducing native species, particularly hardwoods. Under this mandate, the traditional harvesting-planting approach is no longer viable and an alternative approach is needed. Restoring these plantations can also serve as a model system to explore the effectiveness of different restoration practices in a subtropical island environment such as Taiwan's, for which little empirical experience exists.

Thinning (or selective cutting) and understory vegetation control are regularly prescribed in plantation forest management, and such practices may also facilitate forest restoration (e.g., [12]). The partial removal of trees can enhance local light availability and create physical environments similar to canopy gaps, which are essential for seedling survival [14–16]. Because only a portion of the trees are removed, the overall abiotic environment of the stand is usually not altered substantially [17].

The presence of understory vegetation may have both positive and negative effects on the survival of seeds and seedlings [10–12]. The presence of understory vegetation may reduce seedling survival by reducing light availability, by increasing competition between seedlings and understory vegetation, or both [6,8,11]. However, understory vegetation may also reduce seed and seedling predation by providing protection [8,18].

A preliminary feasibility study conducted in 2006 by randomly planting 4-year-old saplings of *Quercus glauca* (Thunberg) Oersted, *Q. longinux* (Hayata) Schottky, *Q. gilva* (Blume) Oersted, *Pasania hancei* (Benth.) Schottky var. *ternaticupula* (Hayata) Liao, and *P. harlandii* (Hance ex Walp.) Oerst. in a Japanese cedar plantation showed encouraging results, indicating that saplings of native, late-successional Fagaceae species can successfully establish [19]. However, compared to planting seedlings or directly sowing seeds, such a practice is clearly more expensive. Therefore, empirical studies are still needed to devise less expensive methods for restoring monospecific Japanese cedar plantations to native mixed hardwood forests.

To fill this knowledge gap, in this study we used a systematic approach to identify critical establishment stages of native broad-leaved species in a Japanese cedar plantation in central Taiwan. We addressed the following two questions: (1) Is seed germination a bottleneck for tree establishment? If so, which silvicultural techniques can improve seed germination? (2) Is seedling survival a bottleneck for tree establishment? If so, which silvicultural techniques can increase survival rates?

We designed three field experiments to answer each of the questions. First, direct seeding was carried out to evaluate seed germination. We sowed both fresh and germinating acorns on the forest floor surface under both closed and opened canopy. Second, given the lack of success in direct seed sowing, we experimented with different methods to prevent seed predation, including seed concealment and chemical repellents, to evaluate if seed predation could be deterred. Third, we planted seedlings of various ages under both closed and opened canopy. In combination with the previous questions, the impact of thinning on hardwood seedlings' recruitment was also evaluated.

2. Materials and Methods

2.1. Study Site

This study was conducted in a 10-ha Japanese cedar plantation in the Heshe District of the National Taiwan University Experimental Forest, central Taiwan (120°52′ E, 23°37′ N, 1442–1602 m.a.s.l.). Based on the information obtained from the nearest weather station (approximately 5 km away), mean annual temperature is 19.8 °C, with a mean annual rainfall of 1500 mm, indicating a warm-humid temperate climate regime.

Originally an evergreen broad-leaved late-successional stage forest dominated by Fagaceae and Lauraceae species, the site was clearcut in 1958 and planted with Chinese fir (*Cunninghamia lanceolata* Hook.). Due to extensive typhoon damages in 1969, the stand was salvaged and replanted with Japanese cedar in 1971. In 2005, the plantation was selected as a demonstration site to study the gradual restoration of Japanese cedar plantations to native forests. Remnants of the native forest can still be found within a 500-m radius from the edges of the plantation. We considered those remnants to represent the reference condition for the restoration project. They set the initial goal for a successful restoration. A preliminary inventory revealed that saplings of the late-successional Lauraceae species (mainly dispersed by birds) were relatively abundant at the study site. However, only a few saplings of Fagaceae species were present. Thus, we decided to focus our efforts only on understanding the bottlenecks for a successful reintroduction of native Fagaceae species. We used acorns collected from the surrounding areas. Because many Fagaceae species display a masting behavior, the study species used every year were determined by the availability of acorns at the time of study.

2.2. Thinning Treatments and Establishment of Transects

In 2005, as part of the preliminary study, 20 percent of the standing volume was thinned to create gaps of various sizes. Then, in 2009, we established four research plots, two in thinned gaps and two in unthinned areas, within the plantation (see Supplementary Information). The canopy openness of the two thinned plots was 27 and 29 percent, whereas the openness of the unthinned plots was 13 and 11 percent. For each plot, a 15-m transect was set at each of the eight cardinal and inter-cardinal directions. We then randomly selected two transects at cardinal directions and two transects at inter-cardinal directions in each plot for manual removal of understory vegetation in a 1-m-wide strip along the entire transect (referred henceforth as devegetated transects). The understory of the remaining two transects was left untouched (referred henceforth as vegetated transects). The experimental schedule for the four consecutive research campaigns is described in Table 1. Detailed diagrams of the experimental spatial design for each plot can be found in the Supplementary Information.

Table 1. Silvicultural treatments (listed by year) tested to enhance the establishment of different Fagaceae species in different annual research campaigns.

Treatment	*Lithocarpus lepidocarpus* (Hayata) Hayata	*Quercus glauca* (Thunberg) Oersted	*Pasania kawakami* (Hayata) Hayata	*Pasania hancei* (Benth.) Schottky	*Pasania harlandii* (Hance ex Walp.) Oerst.
Direct seeding					
Fresh seeds	2009, 2011		2009	2011, 2012	
Germinated seeds	2011	2010		2010, 2011, 2012	
Controlling seed predation					
Fencing		2010	2011 [1]		
Seed concealment	2011			2012	
Chemical repellent				2012	2011
Planting seedlings					
3-month-old				2011	2011
1-year-old		2011		2011	

[1] No data were obtained in 2011 from the fencing experiment due to the breakage of all fences.

2.3. Direct Seeding of Fresh and Germinated Seeds

To detect if seed germination and survival were bottlenecks during the establishment process, we placed acorns of different species every year from 2009 to 2012. We used acorns from different late-successional species relatively abundant in the surrounding areas in each specific year. Eight infrared automatic cameras were installed in the research site, one for each species-treatment combination, to record how and by which animal species the seeds were removed or consumed.

In spring 2009, fresh acorns of *Lithocarpus lepidocarpus* (Hayata) Hayata and acorns of *P. kawakamii* (Hayata) Hayata, each totaling 1920 seeds, were placed on top of the forest floor in thinned and unthinned plots, with and without understory removal (see Supplementary Information). Acorns were checked and the number of remaining seeds was recorded every two days. About a month later, none of the seeds were left [20].

Due to the complete establishment failure in 2009 of fresh acorns, we hypothesized that germinated seeds would be less palatable and, therefore, less attractive to seed predators. Using germinated seeds also ensured that seed quality or viability would not be a factor influencing our results. To get germinated seeds, acorns were gathered in October 2009. In the lab, water was used to separate low quality (floating) seeds from high quality (sinking) seeds. Selected seeds were stored stratified in wet moss at 4 °C until February 2010. Then, pots at the lab were used to bury seeds in soil for one month until March 2010, when they were extracted. Therefore, in spring 2010, germinated seeds (i.e., with radicles just emerging) of *Q. glauca* and *P. hancei* var. *ternaticupula*, each totaling 560 acorns, were placed in thinned and unthinned plots, with and without understory removal (see Supplementary Information). After placing the seeds on top of the forest floor, the number of seeds remaining was counted every other day during the first month. Thereafter, remaining seeds were counted on a monthly basis. After nine months we measured the height and basal diameter of the remaining established seedlings.

To account for potential inter-annual differences, we repeated our experiments in 2011 and 2012. In spring 2011, 560 fresh and 560 germinating seeds from each of two species, *L. lepidocarpus* and *P. hancei* var. *ternaticupula*, were placed in thinned and unthinned plots, with and without understory removal (see Supplementary Information). We placed both germinating and fresh seeds in the same transect line but at different distances. Seeds were checked and the number of remaining seeds was recorded every Monday, Wednesday, and Friday for two months.

In spring 2012, we established 80 monitoring points in an unthinned plot. Among them, we randomly selected 40 points and manually cleared the understory of half of these points. We then put 200 fresh and 200 germinated seeds of *P. hancei* (10 per acorn condition per point) on top of the forest floor (see the Supplementary Information). We monitored the number of remaining seeds on a weekly basis for one month.

2.4. Controlling Seed Predation

Guided by the results of our direct sowing trial, we tested different approaches to reduce acorn consumption. These approaches included using physical barriers, burying seeds with soil and litter, and using chemical repellents.

2.4.1. Physical Barriers

In spring 2010, we built three $1 \times 1 \times 1$ m^3 complete enclosures with polyethylene (PE) mesh. These physical barriers were set up at each transect (combining different canopy and understory types, see above). A hundred fresh *Q. glauca* seeds were placed inside each fenced area. Survival rates were calculated after 3 and 8 months. In spring 2011, a similar experiment was carried out for *P. kawakamii*.

2.4.2. Seed Concealment

In July 2011, 150 fresh *L. lepidocarpus* acorns were placed in three unthinned transects (50 seeds in each) and buried 5 cm below surface, and 150 seeds were also placed on the surface of another three unthinned transects. Seeds were monitored every Monday, Wednesday, and Friday for two months. The experiment was repeated in April 2012. First, 100 fresh and 100 germinated seeds of *P. hancei* were buried 3 cm below surface in unthinned transects. Second, 100 fresh and 100 germinated seeds of the same species were covered with Japanese cedar's litter. Seed status (alive, missing, or dead) was monitored weekly after burial.

2.4.3. Chemical Repellents

Chemical repellents were used in 2011 and 2012 in locations alongside, but outside of, the transects. In April 2011, 1200 seeds of *P. harlandii* were treated with two repellents (Cinnamamide 97% and trans-Cinnamaldehyde 98%) in four concentrations (0.0, 0.4, 0.8, and 1.2% w/w) with five replicates (30 seeds per treatment). Treated seeds were monitored every Monday, Wednesday, and Friday for two months after field placement. In May 2012, 1200 seeds of *P. hancei* were treated with trans-Cinnamaldehyde 98% in four concentrations (0.0, 5.0, 10.0, and 15.0% w/w) with 10 replicates (15 seeds per treatment). Seed status (alive, missing, or dead) was monitored weekly after the treated seeds were placed on the forest floor surface.

2.5. Planting Seedlings of Various Ages

To further investigate potential bottlenecks in Fagaceae species establishment, in April 2011 we planted 1-year-old nursery grown seedlings (less than 1.30 m tall) of *Q. glauca* and *P. hancei*, as well as 3-month-old nursery grown seedlings of *P. hancei* and *P. harlandii* in unthinned and thinned plots. Seven seedlings were planted along each transect of the plots after clearing the understory. The status of seedlings (alive or dead) was checked weekly after planting. Nine months later, we closed the experiment and measured the average basal diameter and height of the surviving seedlings.

2.6. Data Analysis

A semi-parametric approach based on a generalized additive mixed model [21] was used to analyze the seed and seedling survival probabilities of each experiment. We limited our analysis to the first 30 days because most of the surviving seeds of all species used in this experiment fully germinated after that time. In the model, treatment effects were modeled parametrically, whereas the time effect was modeled non-parametrically using a thin-plate regression spline with a smoothing term for each treatment. For all species, a first-order autoregressive model was used to account for the autocorrelation present in the data. We used the R package *mgcv* to perform the analyses [22].

3. Results

3.1. Seed Survival

Although the final results showed that all the acorns were eaten or removed, survival analyses indicated that canopy openness and understory presence had different effects during the removal/consumption processes depending on the species. Silvicultural treatment did not have significant effects on fresh *L. lepidocarpus* and *P. kawakamii* seeds in 2009 (Table 2, Figure 1). However, seeds had different removal rates in 2010 depending on the silvicultural treatment for *P. hancei*, but no differences were found for *Q. glauca* (Figure 2). Seed survival rates for *Q. glauca* over the first 33 days were not significantly different among the treatments. In contrast, the absence of understory cover significantly lowered survival rates for *P. hancei* seeds, whereas canopy openness had no effect (Table 3).

Table 2. Effects of thinning and understory removal on the seed survival rates of *Lithocarpus lepidocarpus* (Hayata) Hayata and *Pasania kawakamii* (Hayata) Hayata. over the first 36 days after fresh seed placement in spring 2009 and 2011.

Treatment	*L. lepidocarpus*			*P. kawakamii*		
	df	χ^2	*p*	*df*	χ^2	*p*
Understory control	1	0.091	0.763	1	0.748	0.387
Thinning	1	1.176	0.278	1	0.238	0.625
Understory control × thinning	1	0.856	0.355	1	1.308	0.253

Table 3. Effects of thinning and understory removal on the seed survival rates of *Quercus glauca* (Thunberg) Oersted and *Pasania hancei* var. *ternaticupula* over the first 33 days after fresh seed placement in spring 2010 and 2011.

Treatment	*Q. glauca*			*P. hancei*		
	df	χ^2	*p*	*df*	χ^2	*p*
Understory control	1	1.128	0.288	1	4.001	0.0455
Thinning	1	0.303	0.582	1	0.010	0.9203
Understory control × thinning	1	0.435	0.509	1	0.109	0.7414

For the 2009 trial, all the fresh seeds were consumed within one month after field placement (Figure 1). In the 2010 trial, 33 days after the germinated seeds were placed, 19.4% to 72.1% of the seeds were still present except for *Q. glauca* seeds in the devegetated transects (Figure 2). By the end of the second month, almost all of the *Q. glauca* seeds disappeared (being either consumed or removed), while some *P. hancei* seeds were still left on the ground. In summary, *Q. glauca* seeds were removed at a faster rate than that of *P. hancei*. For both species, seeds were consumed or removed at a faster rate for transects without understory vegetation in comparison to transects with understory vegetation.

In the 2011 trial, we repeated the same approach as in 2010. Final survival rates for *L. lepidocarpus* seeds detected among the treatments or seed life stage did not significantly differ. However, canopy openness had a significant effect on the survival rates of *P. hancei* seeds (Table 4). Most of the seeds, regardless of whether they were fresh or germinated, were removed in the first week (Figures 1 and 2). In the last trial of 2012, all the seeds left unburied on the forest floor were removed within three weeks, regardless of the germination status and the placement (Figure 3).

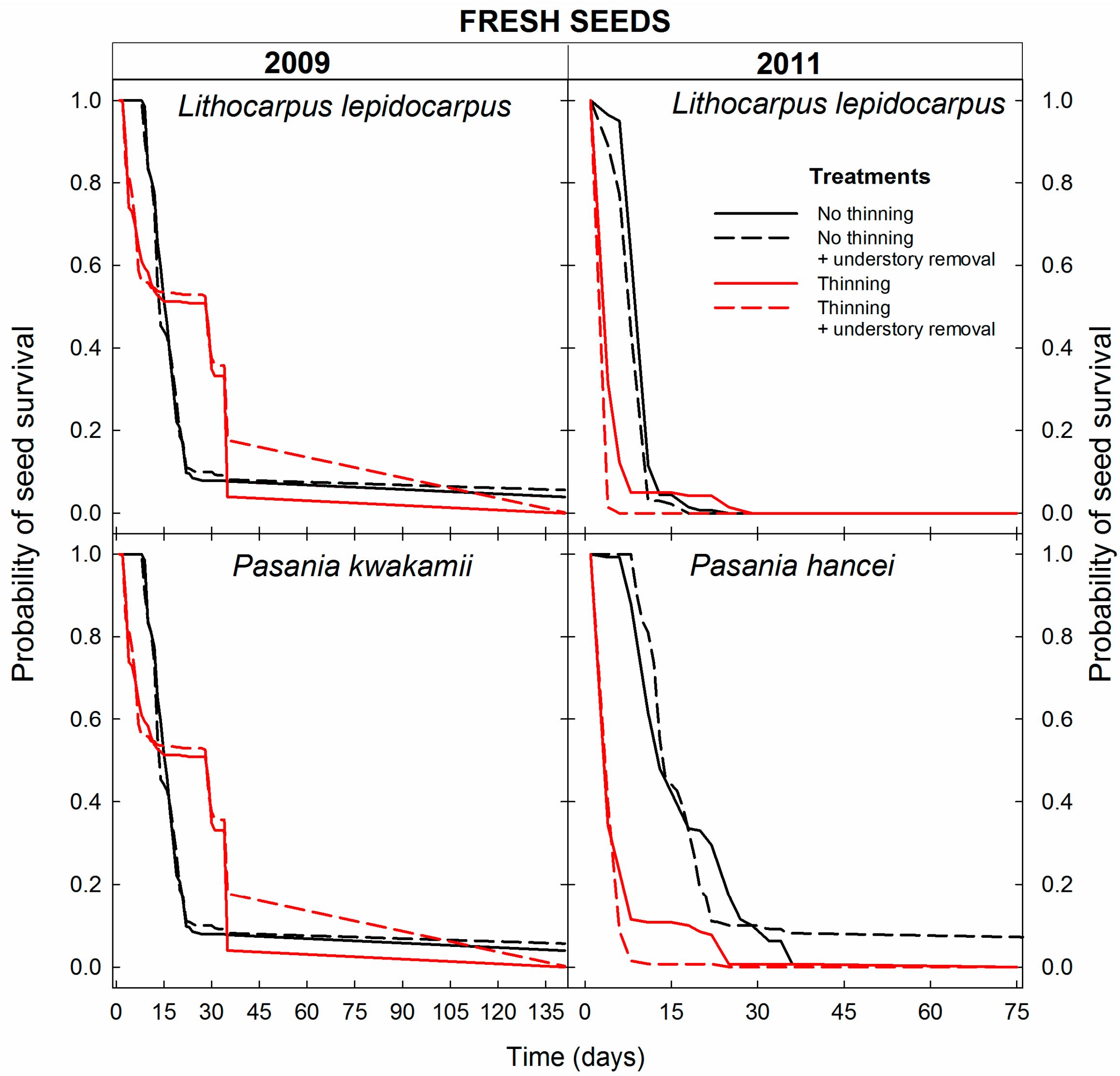

Figure 1. Average survival rates for fresh seeds of three different hardwood species under four different forms of site preparation management. The study was carried in 2009 (**left panels**) and repeated in 2011 (**right panels**).

Table 4. Effects of thinning, understory removal, and seed germination life stage treatments on the seed survival rates of *Lithocarpus lepidocarpus* (Hayata) Hayata and *Pasania hancei* var. *ternaticupula* over the first 36 days after seed placement in spring 2011.

Treatment [1]	*L. lepidocarpus*			*P. hancei* var. *ternaticupula*		
	df	χ^2	*p*	*df*	χ^2	*p*
Understory control	1	2.784	0.0952	1	2.975	0.0846
Thinning	1	0.057	0.8115	1	11.341	0.0008
Type of seeds (fresh or germinated)	1	0.460	0.4979	1	3.441	0.0636

[1] Non-significant interactions were removed from the analysis.

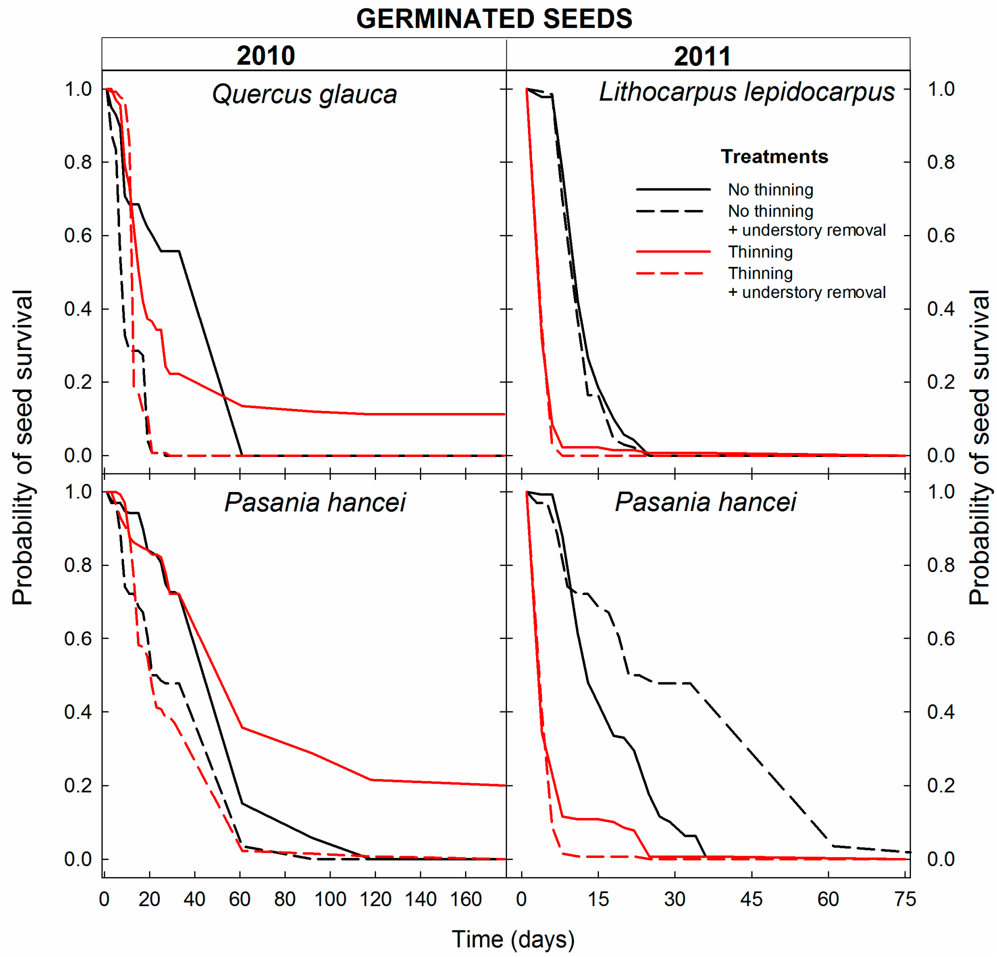

Figure 2. Average survival rates for germinated seeds of three different hardwood species under four different forms of site preparation management. The study was carried in 2010 (**left panels**) and repeated in 2011 (**right panels**).

Results from 2009 to 2011 suggested that the different removal rates were likely due more to the locations of seed placement rather than to the causes of seed removal. However, survival analyses showed that there were significant differences in seed removal rates depending on seed covers for the last year's trial (Table 5). Burying seeds in the mineral soil significantly delayed seed survival, but it did not change the outcome that after 80 days seed survival was also negligible (Figure 3). No significant interactions between canopy openness, understory presence, or seed life stage were detected in any year for any species.

Table 5. Effects of different methods to prevent seed predation (burial under soil, burial with litterfall, no ground vegetation, and control) and seed germination phases (fresh vs. germinated) on the seed survival rates of *Pasania hancei* var. *ternaticupula* over the first 39 days after seed placement in spring 2012.

Treatment [1]	***P. hancei* var. *ternaticupula***		
	df	χ^2	*p*
Method	1	11.884	0.0078
Germination phase	1	0.446	0.5043

[1] Non-significant interactions were removed from the analysis.

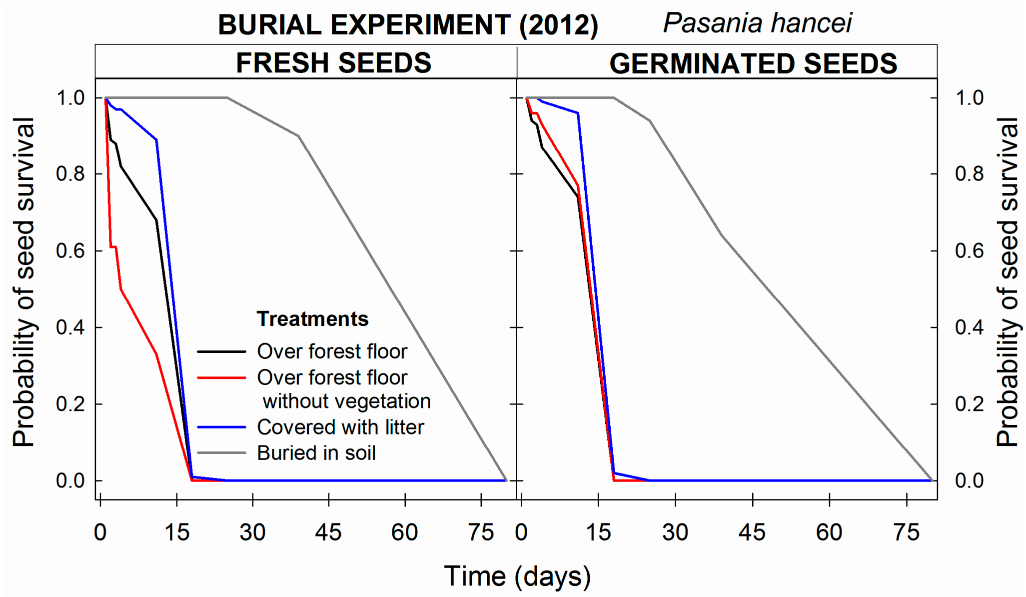

Figure 3. Survival rates of fresh and germinated seeds of *P. hancei* var. *ternaticupula* during the seed concealment experiment carried out in 2012.

3.2. Controlling Seed Predation

3.2.1. Physical Barriers

For the 2010 trial, seedling survival rates inside the fenced areas were 85.0% and 77.7% for the plots without understory (thinned and unthinned sites, respectively) eight months after the beginning of the experiment. However, survival rates were 52.3% and 61.3% for the plots with understory (thinned and unthinned sites, respectively; Figure 4). These results indicated that although understory plays a major role in seed establishment, physical barriers help to prevent acorn consumption. Unfortunately, no survival data from the 2011's trial could be obtained, as all fences were gnawed by rodents, which entered into the fenced areas. Therefore, most of the seeds were consumed, and only 11 seeds germinated.

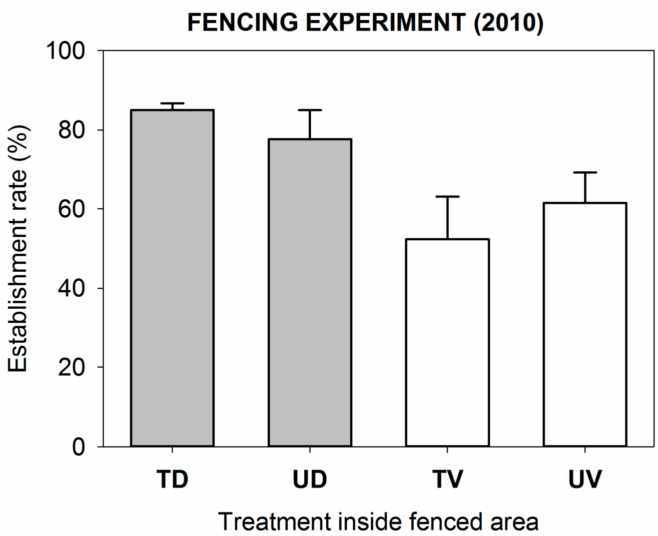

Figure 4. Seed establishment rate after eight months inside the fenced areas in 2010 for four different management regimes: T: thinned canopy; U: unthinned canopy; D: devegetated (understory removal, grey bars); V: vegetated (white bars). Bars indicate average ± standard error.

3.2.2. Seed Concealment and Chemical Repellents

In 2011, all unburied seeds were removed within 2 months, regardless of their germination stage. Four months after burial, 14.4% of acorns were able to germinate and grow to about 25 cm [19]. In 2012, most of the seeds disappeared within 20 days except the ones buried under the soil. However, 80 days after, all the seeds were removed regardless of the treatments. As for the effects of chemical repellents, all seeds disappeared within 3 weeks of the beginning of the experiment in 2011 (Figure 5), and within 15 days in 2012 (results not shown).

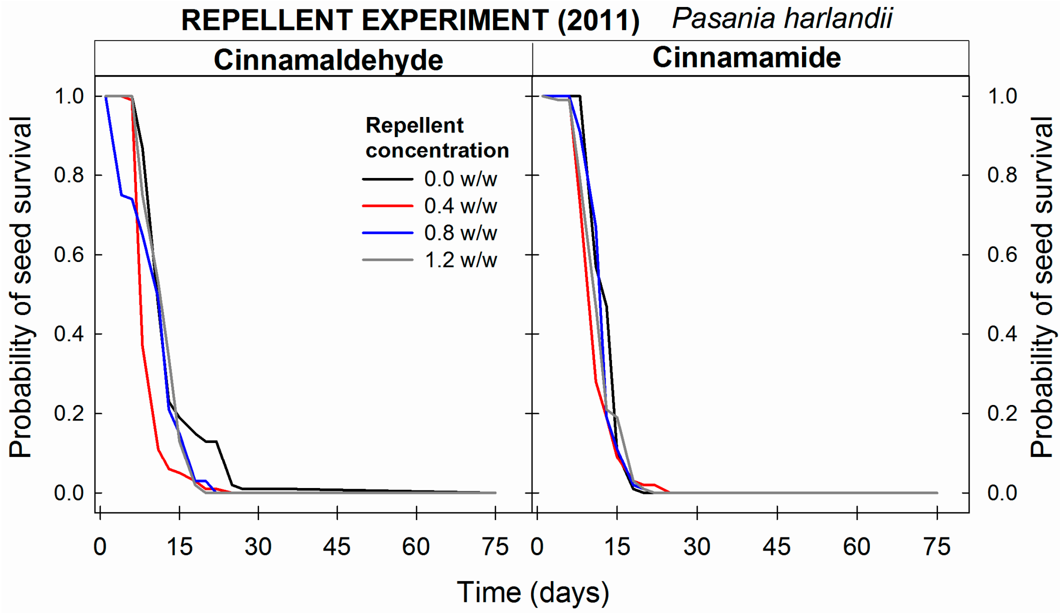

Figure 5. Seed survival rates after the applications of two different chemical repellents at five different concentrations.

3.2.3. Identification of Acorn Consumers

From the images captured by the cameras, we identified five mammal species and five bird species as potential seed consumers or removers during the observation period. The five mammal species were red-bellied squirrel (*Callosciurus erythraeus* Pallas), Formosan ferret-badger (*Melogale moschata subaurantiaca* Swinhoe), spinous country-rat (*Niviventer coxingi* Thomas), Formosan field mouse (*Apodemus semotus* Thomas), and Tada's shrew (*Crocidura tadae* Tokuda & Kano). The five bird species were Eurasian jay (*Garrulus glandarius* L.), Eurasian woodcock (*Scolopax rusticola* L.), bamboo partridge (*Bambusicola thoracica* Temminck), Steere's liocichla (*Liocichla steerii* Swinhoe), and White's ground thrush (*Turdus dauma* Latham). Among the identified faunal species, seed removal behaviors were observed for red-bellied squirrel, Formosan ferret-badger, spinous country-rat, and Eurasian jay.

3.3. Planting Seedlings of Various Ages

Survival rates differed between 1-year-old and 3-month-old seedlings. A very high proportion of 1-year-old seedlings survived until the end of the experiment. In contrast, survival rates of 3-month-old seedlings decreased to 0.2 within 80 days (Figure 6).

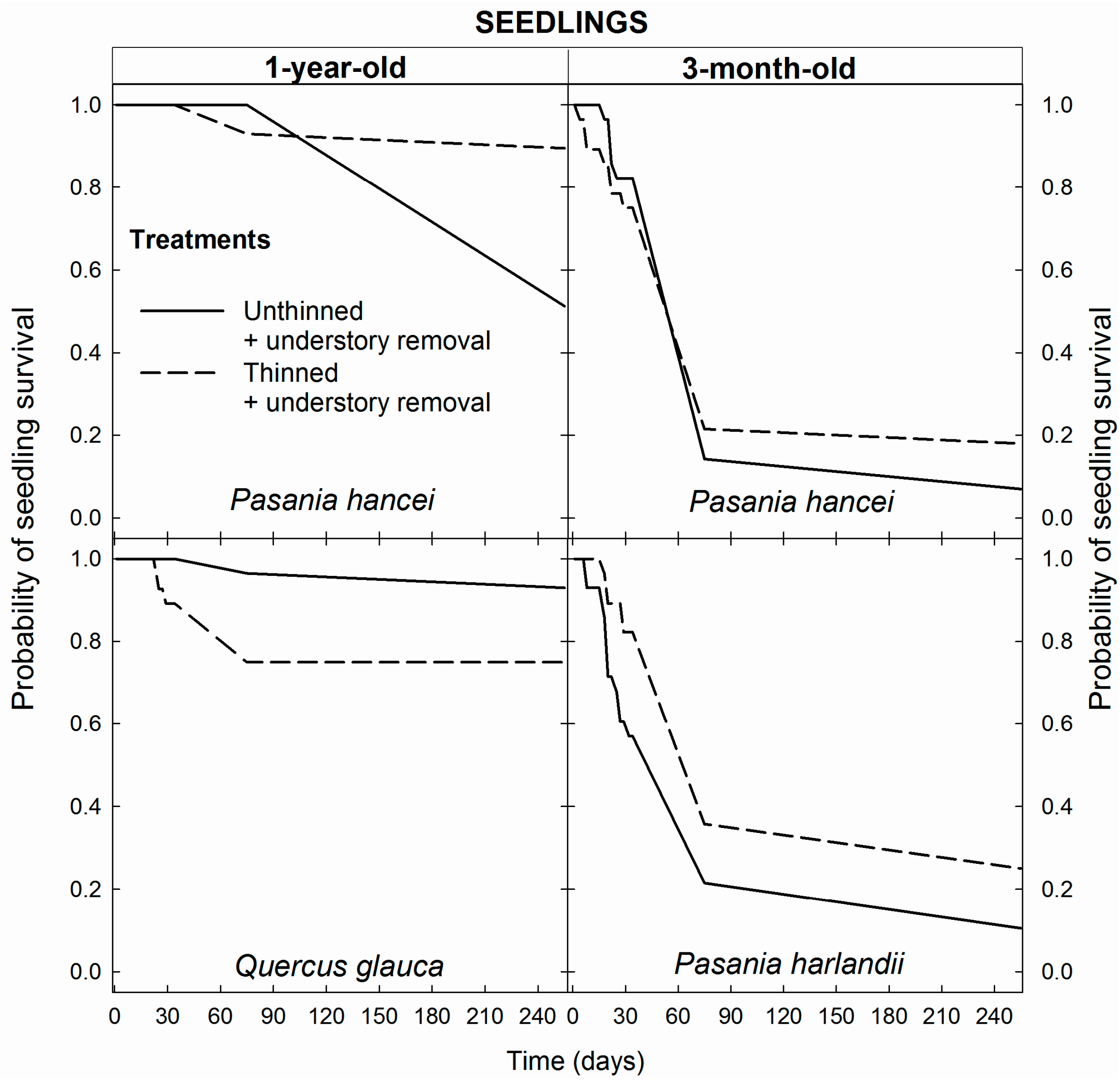

Figure 6. Survival rates of 1-year-old seedlings (**left panels**) and 3-month-old seedlings (**right panel**) of three different hardwood species during the experiment carried out in 2012.

4. Discussion

4.1. Seed Predation as the Main Cause of Establishment Failure

We used a systematic, sequential, adaptive approach to identify bottlenecks for seedling establishment and the best silvicultural treatments to overcome them. Our result from four different years showed that direct sowing (and by similitude, natural seed arrival) was unable to produce viable seedlings. Therefore, some sort of advanced regeneration or seed protection is needed to allow for the establishment of some seedlings if the establishment of native hardwood species is a management objective. Our results suggested that seedlings at least 3 months old, which survived for 3 more months in the field, have the potential to successfully establish at this site, but such survival was guaranteed only when using 1-year-old seedlings.

Seed survival and establishment rates observed in this study were low compared with those found by other studies also done with late-successional or large-seed direct sowing [5,7,13]. These low rates could result from both biotic (e.g., predation) and abiotic (e.g., drought) factors that limited seedling establishment [6,11,13].

The impact of thinning on seed predation has been demonstrated by several earlier studies (e.g., [23,24]). Previous studies have also demonstrated the significant influence of understory vegetation (e.g., [10,25]). However, the effects of canopy openness or the presence of understory vegetation on seed survival are somewhat context-dependent [12,26–28]. Understory can have both positive and negative effects on seed predation. On one hand, increased understory growth could hide the seeds better and facilitate their survival, as the predators need to spend more time finding them. On the other hand, understory could provide cover for other seed consumers that do not go into open areas but can now reach those seeds. Furthermore, some understory species also produce fleshy fruits and may provide additional food resources for seed predators. Depending on the types of seed predators present in the region, seed predation may increase or decrease in different microhabitats after silvicultural treatments [26,27,29]. For instance, seed predation by squirrels is reduced in canopy gaps, whereas predation activities by field mice are higher in canopy gaps [28].

We detected different consumption/removal patterns and different seed predators among years. At the same time, we detected initial differential survival rates for seeds of different growth stages within the first month. Different removal patterns could be due to different foraging behaviors and feeding paths of main seed predators. For example, as captured by camera, red-bellied squirrels tended to systematically remove all the seeds in one spot, and when they depleted all the acorns in that spot, they moved to the next spot. In addition, it has been reported that differences among seeds caused by seed nutrient content, physical and chemical defense mechanisms (e.g., shell hardness, presence of secondary metabolites, etc.) affect the preference of seed feeders [30]. However, our initial hypothesis that germinated seeds would be less favorable for seed consumers was rejected, as no significant differences on seed predation rates between fresh and germinated seeds were detected in the long term (more than two months after direct sowing).

In addition, the lack of a cold winter also means that there are no seasonal patterns in rodent population sizes [31]. Therefore, storing seeds for planting them at the time of lower seed predator population levels does not seem to be a viable option. At these sites, the breeding season for rodents lasts for two-thirds of the year, from January to August. During that time, energy demands are high because of pregnancy and nursing. However, the Japanese cedar plantation is short of food resources. Consequently, the seeds placed by us may have attracted those predators. These circumstances may explain why germinated seeds were also consumed or removed, even at a faster rate than fresh seeds [32]. Both factors will be important considerations in our future research on methods to improve the success of reintroduction programs. It should be highlighted that because the main purpose of this study was to develop effective silvicultural practices to improve seed survival and seedling establishment, we only placed a small number of seeds in the field, as constrained by seed availability and economic considerations. If we had used larger numbers of seeds, the saturation effect could have increased seed survival rates.

Predation is not the only mechanism by which seeds fail to establish. Scatter-hoarding behavior has also been widely observed in squirrels and jays in various forest ecosystems [33,34]. Instead of consuming the seeds, the animals remove the seeds and cache them in a different place. The captured photographs suggested that the major seed predators at the study sites were granivorous animals, including the red-bellied squirrel. Such scatter-hoarding behavior by the granivorous animals may explain the similar seedling establishment rates for *Q. glauca* and *P. hancei* after nine months. Additional species that were observed to remove the seeds were the Formosan ferret-badger, spinous country-rat, and Eurasian jay. However, seed-removal behavior was less frequent in those species than in red-bellied squirrels.

On the other hand, some of these animals may also function as seed dispersers because of their scatter-hoarding behavior. For example, in our study red-bellied squirrels seem to have removed large numbers of the seeds. The seeds that were removed may not have been eaten immediately but may have been stored for later consumption, and the cached seeds may subsequently germinate. In a follow-up expedition to the research sites in April 2017, a few of the placed acorns germinated and established. Interestingly, all those seedlings were a short distance away from their original placement locations.

Finally, climate variability may also contribute to the different observed inter-annual seed mortality patterns. Unlike other Fagaceae species in temperate regions which have other sources to supply soil moisture at the beginning of growing seasons, (e.g., snow melting), Taiwanese species depend entirely on rainfall for soil water availability during that time. The 2009–2010 El Niño event delayed the beginning of the 2010 wet season in central Taiwan for approximately six weeks, and the precipitation amount was below average during the first three months of that growing season. Hence, the first two months of the experiment were probably too dry to allow proper germination, causing the low germination rates and a germination period that was longer than expected.

4.2. Preventing Seed Predation

None of the three approaches used to discourage seed predation worked in a significant way, except physical barriers. Xiao et al. [35] and Chang et al. [36] also showed that using enclosures as physical barriers is a feasible way to increase establishment rates. Similar to the results reported by those authors, our preliminary tests also showed that seed germination rates inside the fenced areas were similar to rates obtained in the lab (data not shown). However, if we apply this method to larger areas, restoration costs will increase significantly, and could produce other undesirable ecological effects such as hindering the mobility of some wildlife species [37]. More importantly, the effect was inconsistent, as it only worked in 2010, but failed in 2011. Our 2011 results suggested that the seed-predators might have "learned" ways to overcome the barriers.

In addition to protecting the seeds from their predators with nets, we also used soil or litterfall to conceal the seeds to prevent seed predator detections. Compared to directly placing the seeds on the forest floor surface, burying seeds can slow removal rates, provide a better micro-environment for germination, and increase seedling survival and establishment rates [38–41]. In our first seed concealment trial, most of the seeds remained under the soil and had a 14.4% seedling establishment rate. These results are very similar to other previously reported results [42]. However, the protection was inconsistent, as in our second year's trial all the seeds were consumed within 80 days after burying them. Therefore, although burying seeds has the potential effect of reducing seeds from being found and consumed, such a benefit is not guaranteed.

Regarding chemical repellents, they did not have any noticeable effect on discouraging seed predators, particularly rodents, opposite to reports by some studies [43–45]. A possible explanation for this contradictory result could be that the rodents in Taiwan (e.g., red-bill squirrel or stripe squirrel) have a high tolerance to the food they eat [46,47]. Therefore, chemical repellents do not work as well as in other places. Another possible explanation is that both chemicals could have evaporated or washed out by rain a few days after application, hence lowering their concentrations to the levels where they became ineffective as repellents.

Finally, it should be taken into account that the management history of the site and surrounding region has caused the disappearances of keystone predator species that can regulate rodent populations' levels, thus creating a cascading effect on Fagaceae seeds.

4.3. Overcoming Establishment Bottlenecks: Ecosystem Management Implications

Our results indicated that the main establishment limitation is the fast removal of seeds, usually in less than a month. Similar results have been described before [48,49]. From our results, it seems clear that restoring these Japanese cedar plantations using only seeds is not effective, and therefore older seedlings should be used.

Comparing the establishment rates between 3-month-old and 1-year-old seedlings, older seedlings have higher survival and establishment rates. The effects of canopy conditions depend on seedling ages. An open canopy increased the establishment rates for young seedlings, but the situation was reversed for older seedlings. This difference could be due to a higher variety of micro-environments and understory vegetation in the thinned site, which also led to variations in seed predators' population sizes and feeding paths [50,51]. Young seedlings are less conspicuous and harder to find when the environment is more heterogeneous. In addition, thinning could increase light levels and therefore enhance the growth of shade-tolerant understory species [52]. However, understory vegetation was relatively dense at the study site, possibly because of the improved light conditions following the thinning. Although potentially beneficial for seeds, understory vegetation could be detrimental to older seedling survival, due to competition for water, nutrients, light, and growing space [53].

Seedling mortality causes also differed for seedlings with different ages. The major cause of death for 3-month-old seedlings was biting and chewing. Young seedlings still had a part of the acorn (large, more nutritious part) attached to the plants. Therefore, after seed predators finish eating all the available seeds in the area, they can turn to young seedlings to eat the remnants of seeds attached to the young plants, particularly if there is still pressure on food sources in the field. However, this situation is not applicable to 1-year-old seedlings, in which seed remnants have already fallen or decomposed, and their stems were more woodified. As a consequence, the major cause of death for older seedlings was withering (mostly by drought), similar to other studies [11].

From a management perspective, while opening the canopy and maintaining plant cover is important during the first months of the restoration effort, after seeds have been able to get established and survived their first year, understory should be controlled or removed to reduce competition for growth resources. The use of these techniques is the next natural step for developing our adaptive empirical approach to establish restoration guidelines at our study sites.

The native late-successional forests in the study area were originally dominated by hardwood species belonging to the Fagaceae and Lauraceae families. Although the Lauraceae species seem to have the capacity to establish themselves under the canopy of Japanese cedars, this is not the case for Fagaceae species. Although many Fagaceae trees with abundant seeds can be found in remnant stands near the study site, naturally regenerated seedlings and saplings are rare at the site, suggesting that recruitment is strongly limited, as our results confirm. All signs suggest that in the absence of human intervention these abandoned plantations would not be able to return to their original state, at least in any time soon. Once a forest ecosystem has been altered in a substantial way, ecosystem-level restoration measures are necessary. For example, although not tested in the current study, a potential method to reduce seed predation pressure is to re-introduce the now locally extinct natural higher-level (e.g., carnivorous) predators into the plantations to control seed predators.

5. Conclusions

This study represents the first attempt to identify establishment bottlenecks for Fagaceae species in conifer plantations in Taiwan. Our experiments indicated that without some kind of human intervention, it will take a long time (i.e., via succession) for Fagaceae species to establish in Japanese cedar plantations that are no longer serving their purposes. Among the methods tested to bring native Fagaceae species back, direct sowing was shown to have the lowest survival and seedling establishment rates, whereas seedling planting had a higher survival rate. Direct seeding with fresh seeds was observed to be virtually useless. The final survival rates from high to low were 1-year-old seedlings, 3-month-old old seedlings, germinated seeds, and fresh seeds. Seedlings older than 6 months were observed to be able to successfully establish in this site. Burying germinated seeds, in combination with thinning and a proper understory vegetation control was able to delay seed consumption but did not prevent it. Our results indicated that fencing with rodent-resistant material seems to be the only management option that is likely to result in a majority of seeds getting established. Therefore, if there are important economic or ecological limitations that prevent the use of fences, and some level of risk is accepted, we suggest burying germinated seeds (an easy-to-implement and relatively inexpensive method) as a first test to facilitate the re-introduction of native late-successional Fagaceae species in conifer plantation forests in Taiwan. If unsuccessful, more costly options should be used: either creating fenced areas or planting seedlings that are at least 6 months old.

Supplementary Materials: The following supplementary materials are available online at www.mdpi.com/1999-4907/9/1/3/s1, Figure S1: Location of the four experimental plots in the National Taiwan University Experimental Forests; Figure S2: Experimental design for the placement of seeds at the four research plots used in 2009; Figure S3: Experimental design for the placement of seeds at the four research plots used in 2010; Figure S4: Experimental design for the placement of seeds at the four research plots used in 2011; Figure S5: Experimental design for the placement of 1-year-old seedlings at the four research plots used in 2011; Figure S6: Experimental design for seed concealment experiment with seeds of *Pasania hancei* var. *ternaticupula* (Hayata) Liao in 2012.

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