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Synergistic Effect of Dwarf Bamboo Flowering and Wild Boar Rooting on Forest Regeneration

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Abstract: *Sasa* spp., monocarpic dwarf bamboos, are known to form recalcitrant understories, lower species diversity, and hinder forest development. *Sasa borealis* distributed throughout Korea showed a phenomenon of synchronized dieback after large-scale synchronized flowering nationwide around 2015. Therefore, we conducted this study to take advantage of the rare event and add prevailing activity of wild boars and culm removal to elucidate whether they promote the regeneration of a long-term suppressed forest. We set permanent plots in forests with different understory types, and tracked the vegetation change in 5 years with respect to species composition, tree regeneration, and *S. borealis* reestablishment. This study focused on comparison between plots established after mass flowering. In flowering stands, we found the species diversity increased significantly with increase in species evenness, but not with recruitment of new species. Furthermore, the seeds of mass-produced bamboo germinated, and the seedling abundance was found to increase considerably. In stands rooted by wild boar, species diversity increased through the recruitment of new species, including tree species. It increased the abundance of shrub and perennial herbs, while it suppressed the reestablishment of *S. borealis*. Although rooting effect was independently significant regardless of flowering, the synergistic effect of rooting and flowering on forest regeneration was outstanding. Wild boar seemed to function as a remover of dead culms and a breaker of remaining underground mats as well as a seed disperser. Consequently, the species composition became similar to the reference stands. However, culm cutting caused negative effects by facilitating *S. borealis* to re-occupy or resprout. Overall, as the wild boar population increases, the positive effect can be expected to enhance. At landscape scale, considering several factors such as flowering and non-flowering, and population size of wild boar, the long-term suppressed forests by *S. borealis* are projected to regenerate with mosaic forests.

Keywords: arrested succession; cutting; recalcitrant understory; rooting; biodiversity; semelparity; simultaneous flowering

1. Introduction

Some plant species enable the formation of dense monospecific understory when ample light is exposed to the forest floor due to large-scale and repeated canopy disturbances. Royo and Carson defined it as 'recalcitrant understory' [1]. Such understory is promoted by changes in browsing and fire regime, and is extensively prevalent across several climate zones in temperate [2–6], tropical [7,8], and boreal forests [9].

The well-known species forming recalcitrant understory are ferns, bamboos, lianas, grasses, and *Rhododendron* spp., which expand rapidly via clonal strategy. It should be noted that the understory has negative impacts on forests, such as hindering forest regeneration [10,11], lowering species diversity [1,12–14], inhibiting the establishment and

growth of tree species, and/or acting as environmental sieve that differentiates certain species [4,15–22].

Sasa spp., dwarf bamboos, are typical plants that form recalcitrant understory in East Asia, such as Korea, Japan, China, Sakhalin, and Kuril Islands [23]. These bamboos are widespread and dominate these regions, for example, *Sasa kurilensis* occupied 89% of the forest area and 28% of the woody biomass in Hokkaido, Japan in the 1980s [24]. Past studies reported that anthropogenic disturbances such as loggings have promoted rapid expansion of the *Sasa* spp. [25–27]. In Korea as well, *Sasa* spp. are very common, and particularly, *Sasa borealis* (Hack.) Makino and Shibata dominate in the understory of the forests across the Korean Peninsula, including the national parks [28–31]. This has been regarded as a problematic species which significantly suppresses forest development [14,32].

The recalcitrant understory can last for a long time even after the canopy is closed. Furthermore, it can be maintained even if severe disturbances occur in the forest canopy [33,34]. In contrast, seedlings of other species trapped in a dense understory do not receive enough light even if a canopy gap is formed [35,36]. Therefore, direct disturbances in the understory as well are needed to reduce the negative impact and to restore forest diversity. In particular, temperate deciduous forests lack light resources in the understory [37–39]. Therefore, reducing the competition for light can have a positive effect on forest regeneration [40–42]. Cutting or removing the understory vegetation is one such way because then new species can be established [43,44] and the seedling density of tree species increases [21].

Depending on the functional trait of the species forming the understory (e.g., evergreen, deciduous, or monocarpic), there may be also opportunities for regeneration [1]. For example, deciduous species mainly block light only during growing season, which provides an opportunity for early settlement of spring ephemeral plants [45]. However, this approach is not applicable for *Sasa* spp. because *Sasa* spp. are evergreen and have year-round effects.

Therefore, two measures can be considered to break the understory and reduce their impact. One is to take advantage of the monocarpic nature of the dwarf bamboos. They flower simultaneously over a large area after a long vegetative period around 60 years and thereafter decline simultaneously [46]. There were reports that forest regeneration was promoted after the dieback of *Sasa* spp. due to flowering in Japan [3,47,48]. Although *S. borealis* is distributed nationwide in Korea and has a huge impact on forests, no large-scale flowering has been reported. However, it bloomed all over the country around 2015 and the dieback phenomenon was reported [31,49]. The second measure is to take advantage of animal activities. It has been found that wild boars frequently dig up underground vegetation including *S. borealis* patches to find food [50]. The massive underground rhizome network of *S. borealis* was cut off and excavated [50–52].

The present study was conducted to explore the effect of the very rare opportunity of the synchronized flowering and dieback of *S. borealis* on forest regeneration. Additionally, the effects of wild boar rooting and culm removal were also taken into consideration. Permanent plots were set up in the forests with different understory types by flowering in 2015, rooting and culm cutting, and tracked the vegetation change in 5 years with respect to species composition, tree regeneration, and *S. borealis* reestablishment. This study focused on comparison between plots established after mass flowering. We set four hypotheses in the current study. First, dieback of *S. borealis* will induce natural regeneration of the forest. Second, the rooting activity of wild boar will accelerate the regeneration. This is because it removes not only the culms, but also the underground network. Third, wild boars will also hinder the reestablishment of *S. borealis*. Since seeds are mass-produced after the flowering, there is a possibility to resettle. Fourth, the removal of the culms will help the forest regeneration to some extent by improving the light environment.

2. Materials and Methods

2.1. Study Area and Species

This study was conducted at Mt. Jeombongsan (38°2′56.25′′ N, 128°25′31.36′′ E), one of the peaks in Seoraksan National Park (38°7′10.41′′ N, 128°27′56.02′′ E). It is located on the border of Inje-gun and Yangyang-gun, Gangwon-do in Republic of Korea. Being in a cool temperate climate zone, this region observes an average annual rainfall (1981~2010, 30 years, Inje meteorological station) of 1210.5 mm (January: 17.5 mm, August: 294.0 mm), and annual temperature of 10.1 °C (January: −5.2 °C, August: 23.3 °C) [53]. It is one of the high biodiversity areas with deep weathered granite soil [54]. Here, 86% of the forest is dominated by *Quercus mongolica*, and depending on its location, *Betula costata*, *Juglans mandshurica*, *Pinus densiflora*, *Fraxinus mandshurica*, *Kalopanax septemlobus*, and *Tilia amurensis* are co-occurring.

Since Mt. Jeombongsan is remote, roads were not paved until the 1990s and relatively minimal anthropogenic disturbance existed. However, slash-and-burn farming was prevalent [55]. After the farming was banned in the 1970s, forests started restoring, and it is presumed that *S. borealis* prospered and spread since then. The *S. borealis* occupies a large area, accounting for 35.5% of the total forested area of 2675 ha [56]. It often forms densely-culmed, well-demarcated circular patches, but it also expands, occupying several hectares of slopes (Figure 1) [31]. In *S. borealis*, large-scale synchronous flowering occurred around 2015. We found that 76% of the investigated patches flowered in early summer of 2015 and declined that year [49].

Figure 1. *S. borealis* population occupying the understory of closed forests. (**a**) Non-flowering *S. borealis* patch and (**b**) synchronous dieback of *S. borealis* following the synchronous flowering event in 2015.

Among the medium and large sized mammals distributed at Mt. Jeombongsan, wild boar is the most common [57], which dig up the underground and damage vegetation. Rooted traces by wild boar was very frequently found, suggesting an important role in the dynamics of the forest floor [52]. This would be somewhat similar to how the numerous pits formed by windblown function as microsites for seed germination and establishment [58–60]. The food source of wild boars varies according to season. In winter-spring, when the aboveground food becomes scarce, they mainly feed on underground food sources, such as root, bulbs, tubers, and fallen fruits [61].

2.2. Experimental Layout and Permanent Plot Set Up

To understand the effects of flowering, wild boar rooting, and culm cutting on forest regeneration, an experimental layout was designed at *S. borealis* patches in *Quercus*-dominated forests (Figure 2). Permanent plots with six understory types, viz. flowering (F) or non-flowering (N), rooting (R) or intactness (I), and cutting (C) or intactness (I) were set

up in June 2017 to monitor the changes in vegetation. In addition, a reference understory was considered where *S. borealis* is not present (Ref).
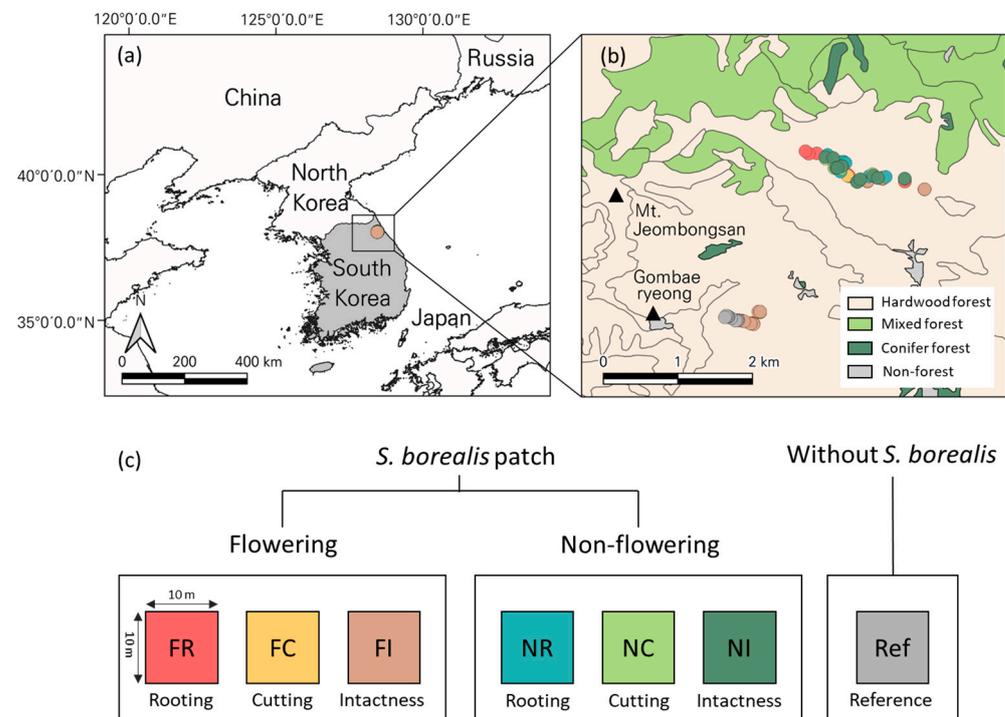
Figure 2. Study area and stand layouts. (**a**) Location of Mt. Jeombongsan in Seoraksan National Park in the Korean peninsula, (**b**) map of the study sites (circle) at Mt. Jeombongsan. Refer to (**c**) for the color code of the study sites and (**c**) layout of seven understory types according to *Sasa* flowering, wild boar rooting activity, and culm cutting. FR: flowering and rooting, FC: flowering and cutting, FI: flowering and intactness, NR: non-flowering and rooting, NC: non-flowering and cutting, NI: non-flowering and intactness, Ref: reference.

'Flowering (F)' referred to the patches where *S. borealis* bloomed and thereafter the culms withered in the same year. The underground was likely to be alive for some years. All of the flowering patches that we set up bloomed in early summer 2015. 'Rooting (R)' referred to the patches dug up and rooted by wild boars in the spring of 2017. Wild boars cut off underground rhizomes and roots, as well as culms. 'Cutting (C)' referred to patches where the culms were cut closest to the ground in August 2017. An additional 0.5 m from the plot boundary was also removed. 'Intactness (I)' referred to patches in which no rooting or cutting happened. The reference understory ('Ref') included neighboring regions where *S. borealis* is not distributed and had no events such as rooting or cutting.

For each understory type, 10 plots, each of dimension 10 m × 10 m plots were set, making a total of 70 plots. In order to minimize disturbance by researchers, each plot was further divided into five subplots of 2 m × 10 m. Three subplots were investigated, and two in between were used as workspaces. All plots were set on slopes of 5° to 35° at an elevation between 700 and 1100 m (Table 1). The vertical extent of the forests was divided into five strata based on the height, namely canopy: ≥8 m, subcanopy: 5~8 m, 1st shrub: 2~5 m, 2nd shrub: 0.5~2 m, herbaceous: <0.5 m. All of them were fairly closed forests with more than 80% coverage of the canopy stratum. *Quercus mongolica* dominated the most, while *Acer pseudosieboldianum*, *Acer pictum* var. *mono*, *Tilia amurensis*, *Cornus controversa*, *Fraxinus rhynchophylla*, and/or *Carpinus cordata* co-occurred (Table 1). The coverage of herbaceous stratum was more than 90% in non-flowering *S. borealis* stands (NI). Conversely, in flowering stands, the coverages were only 6.5% (FC) and 6.2% (FI) due to dieback of the culms. In 2017, two years after the flowering, most of dead culms stood without falling. In the rooted stands (FR and NR), the coverage of herbaceous and litter strata was low due

to the rooting effect. The structures of the cutting stands (NC and FC) were investigated before cutting.

Table 1. Stand characteristics and forest structure at the permanent plots measured in 2017.

Properties	Flowering and Rooting (FR)	Flowering and Cutting (FC)	Flowering and Intactness (FI)	Non-Flowering and Rooting (NR)	Non-Flowering and Cutting (NC)	Non-Flowering and Intactness (NI)	Reference (Ref)
Topography							
Elevation (m)	868~967 [1]	793~962	793~959	882~923	874~921	874~919	965~1054
Slope (°)	12.3 ± 1.4 [2]	24.0 ± 3.1	23.5 ± 2.9	8.2 ± 1.2	17.5 ± 1.5	17.0 ± 1.5	32.5 ± 2.0
Forest structure							
Canopy (%)	88.6 ± 2.1	84.0 ± 3.2	91.5 ± 1.1	91.2 ± 1.4	93.0 ± 1.1	93.0 ± 1.1	91.0 ± 2.9
Subcanopy (%)	35.8 ± 4.7	46.7 ± 7.5	42.5 ± 5.9	50.0 ± 6.0	41.7 ± 6.9	40.7 ± 5.1	34.5 ± 5.6
1st shrub (%)	30.5 ± 6.9	25.9 ± 6.2	18.7 ± 5.3	33.7 ± 5.5	33.6 ± 4.8	36.8 ± 5.6	14.9 ± 2.9
2nd shrub (%)	16.9 ± 4.5	20.1 ± 8.4	22.2 ± 5.0	9.1 ± 2.5	12.3 ± 3.5	12.5 ± 3.2	15.8 ± 4.7
Herbaceous (%)	10.7 ± 1.7	6.5 ± 1.0 [3]	6.2 ± 2.4	36.1 ± 4.1	95.1 ± 1.6 [3]	91.6 ± 2.4	76.3 ± 6.2
Litter (%)	57.0 ± 7.3	97.0 ± 1.1	91.0 ± 1.1	69.0 ± 2.8	100.0 ± 0.0	100.0 ± 0.0	91.0 ± 3.6

[1] Range (min~max), [2] average ± standard error (n = 10), [3] investigated before cutting at FC and NC.

2.3. Vegetation Survey

Vegetation at the permanent plots was annually surveyed during the summer 2017–2020. The vascular plant species and their percentage coverage were visually estimated in the herbaceous stratum. The number of tree seedlings (≥10 cm in height, estimated to settle after 2015) was counted in the subplots (2 m × 10 m). The number and height of the seedlings of *S. borealis* (germinated after 2015) were obtained from the three fixed subplots (1 m × 1 m) in only the flowering patches (FR, FC, and FI). The height of *S. borealis* seedlings was measured for three individuals per subplot.

2.4. Data Analysis

Shannon-Weiner index (H′ = $-\sum p_i \log_{10} p_i$, p_i = relative coverage) was used as the species diversity index. Evenness (E) was calculated from E = H′/$\log_{10}$R, where R (richness) is the number of species. The species composition of the seven understory types was compared with nonmetric multidimensional scaling (NMS) using Sorensen distance. The coverage of plant species that presented in the herbaceous stratum (<0.5 m in height) was converted to a value of 0~1, then transformed into arcsine square-root. The species that appeared in less than three plots were excluded. The significant difference in species composition among the seven understory types was tested with multi-response permutation procedure (MRPP). The NMS and MRPP were analyzed using the PC-ORD ver. 6 [62].

The difference between the group means were tested using analysis of variance (ANOVA) and repeated measures ANOVA. The Bonferroni post-hoc analysis was done when necessary. The data from the reference stands were not included in the statistical analysis. The effect of cutting was tested using data from 2018 to 2020 as the cutting was done in August, 2017. The difference in coverage, height, and density of *S. borealis* seedlings according to understory type (FR, FC, and FI) within the same year was tested by one-way ANOVA using SPSS [63].

3. Results

3.1. Species Diversity

S. borealis flowering (F = 69.151, $p < 0.001$) and wild boar rooting (F = 38.045, $p < 0.001$) contributed significantly to the increase in species diversity in the herbaceous stratum (Table 2, Figure 3a). The evenness showed marked increase with flowering (F = 91.063, $p < 0.001$) and rooting (F = 29.463, $p < 0.001$, Figure 3c). However, only rooting effect was significant for the increase in richness (F = 32.088, $p < 0.001$, Figure 3b), and flowering alone did not increase the richness. For the flowering and rooted stands (FR), the three indices displayed the highest values except for the reference stands (Ref) (Figure 3). The culm

cutting did not significantly affect any diversity indices (Table 2). For NC, evenness was high after cutting in 2018, but as the culms resprouted, it decreased in 2020 (Figure 3c).

Table 2. Repeated measures analysis of variance for the effects of flowering, rooting, and cutting on species indices.

	Source	F-Value	*p*-Value
	Year	31.334	<0.001
	Year × Flowering	1.146	0.289
	Year × Rooting	4.099	<0.05
	Year × Cutting	8.987	<0.01
	Year × Flowering × Rooting	5.099	<0.05
Species diversity	Year × Flowering × Cutting	4.366	<0.05
	Flowering	69.151	<0.001
	Rooting	38.045	<0.001
	Cutting	1.260	0.267
	Flowering × Rooting	0.783	0.380
	Flowering × Cutting	0.929	0.339
	Year	6.132	<0.05
	Year × Flowering	0.063	0.802
	Year × Rooting	14.318	<0.001
	Year × Cutting	0.240	0.626
	Year × Flowering × Rooting	1.048	0.310
Species richness	Year × Flowering × Cutting	0.240	0.626
	Flowering	0.014	0.906
	Rooting	32.088	<0.001
	Cutting	0.013	0.910
	Flowering × Rooting	1.961	0.167
	Flowering × Cutting	<0.001	0.990
	Year	40.780	<0.001
	Year × Flowering	1.810	0.184
	Year × Rooting	1.464	0.231
	Year × Cutting	10.806	<0.01
	Year × Flowering × Rooting	3.328	0.074
Species evenness	Year × Flowering × Cutting	2.643	0.110
	Flowering	91.063	<0.001
	Rooting	29.463	<0.001
	Cutting	1.509	0.225
	Flowering × Rooting	<0.001	0.995
	Flowering × Cutting	1.575	0.215
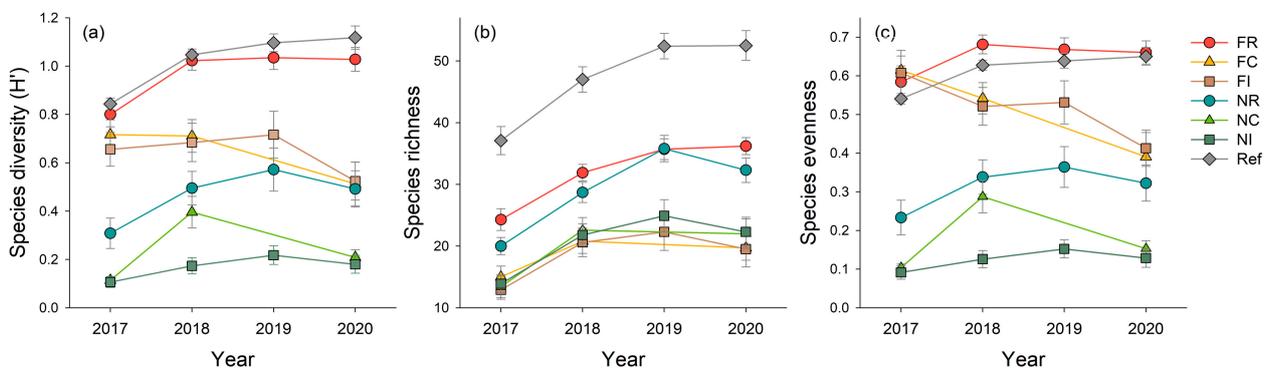
Figure 3. Stand-based species diversity indices in the stands with seven understory types over time. (**a**) Species diversity, (**b**) species richness, and (**c**) specie evenness. FR: flowering and rooting, FC: flowering and cutting, FI: flowering and intactness, NR: non-flowering and Rooting, NC: non-flowering and cutting, NI: non-flowering and intactness, Ref: reference. Values are average ± standard error.

3.2. Species Composition

The species composition of 2017 and 2020 at the seven understory types was analyzed via NMS (Figure 4). The Ref stands without *S. borealis* plants showed a clear difference in species composition located at the left end of axis 1, while other stands, except the rooted stands, occupied the right side of the axis 1. Two rooted stands (FR and NR) along with Ref were located at the left side of the axes 1. They moved even closer to the Ref, indicating that they share similar species composition and/or are similarly abundant.
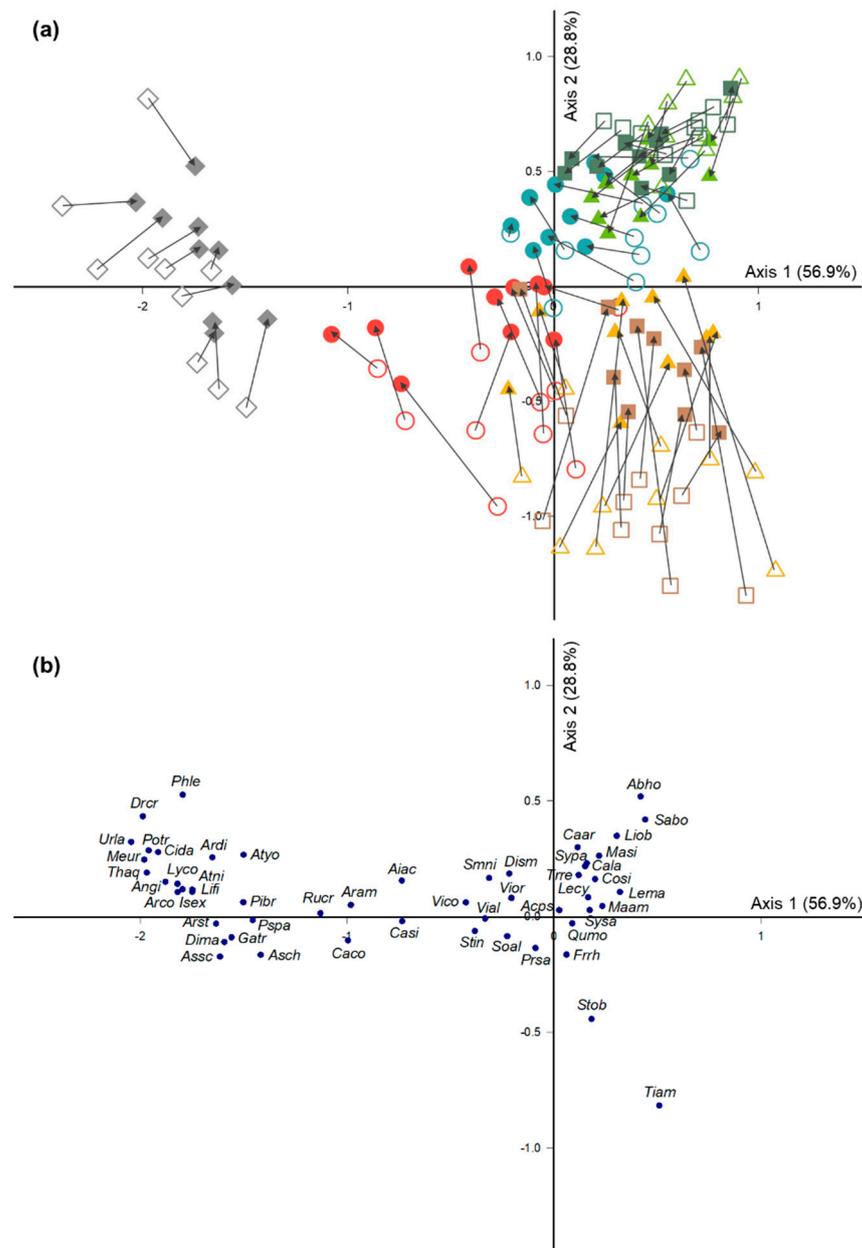
Figure 4. NMS ordination in the stands with seven understory types. (**a**) Stand ordination, (**b**) species ordination. The number next to each axis means the percentage of variance, and the stress of both axes was 0.12 (*n* = 140). Species composition between 2017 (open symbol) and 2020 (closed symbol) is connected by a line with an arrow. Out of the 133 species that occurred in total, only 53 species with a total coverage of all plots (2017 and 2020) of 5% or more were presented. ●: FR (flowering and rooting), ▲: FC (flowering and cutting), ■: FI (flowering and intactness), ●: NR (non-flowering and rooting), ▲: NC (non-flowering and cutting), ■: NI (non-flowering and intactness), ◆: Ref (reference).

Abho: *Abies holophylla*, *Acps*: *Acer pseudosieboldianum*, *Aiac*: *Ainsliaea acerifolia*, *Angi*: *Angelica gigas*, *Aram*: *Arisaema amurense*, *Arco*: *Aralia cordata* var. *continentalis*, *Ardi*: *Aruncus dioicus* var. *kamtschaticus*, *Arst*: *Artemisia stolonifera*, *Asch*: *Astilbe chinensis*, *Assc*: *Aster scaber*, *Atni*: *Athyrium niponicum*, *Atyo*: *Athyrium yokoscense*, *Caar*: *Calamagrostis arundinacea*, *Caco*: *Carpinus cordata*, *Cala*: *Carex lanceolata*, *Casi*: *Carex siderosticta*, *Cida*: *Cimicifuga dahurica*, *Cosi*: *Corylus sieboldiana*, *Dima*: *Diarrhena mandshurica*, *Dism*: *Disporum smilacinum*, *Drcr*: *Dryopteris crassirhizoma*, *Frrh*: *Fraxinus rhynchophylla*, *Gatr*: *Galium trifloriforme*, *Isex*: *Isodon excisus*, *Lecy*: *Lespedeza cyrtobotrya*, *Lema*: *Lespedeza maximowiczii*, *Lifi*: *Ligularia fischeri*, *Liob*: *Lindera obtusiloba*, *Lyco*: *Lychnis cognata*, *Maam*: *Maackia amurensis*, *Masi*: *Magnolia sieboldii*, *Meur*: *Meehania urticifolia*, *Phle*: *Phryma leptostachya* var. *oblongifolia*, *Pibr*: *Pimpinella brachycarpa*, *Potr*: *Polystichum tripteron*, *Prsa*: *Prunus sargentii*, *Pspa*: *Pseudostellaria palibiniana*, *Qumo*: *Quercus mongolica*, *Rucr*: *Rubus crataegifolius*, *Sabo*: *Sasa borealis*, *Smni*: *Smilax nipponica*, *Soal*: *Sorbus alnifolia*, *Stin*: *Stephanandra incisa*, *Stob*: *Styrax obassia*, *Sypa*: *Syneilesis palmata*, *Sysa*: *Symplocos sawafutagi*, *Thaq*: *Thalictrum aquilegifolium* var. *sibiricum*, *Tiam*: *Tilia amurensis*, *Trre*: *Tripterygium regelii*, *Urla*: *Urtica laetevirens*, *Vial*: *Viola albida*, *Vico*: *Viola collina*, *Vior*: *Viola orientalis*.

On the right side of the axis 1, non-flowering patches were located on the upper side of axis 2, while the flowering patches were located on the bottom. This indicated that the species composition differed considerably depending on whether the stands were flowering or not. However, for both flowering and non-flowering stands, the cutting had little effect on species composition. Therefore, the differences in species composition between FC and FI, and NC and NI were not statistically significant (MRPP: $p > 0.05$). Other than that, all were found to be statistically significant ($p < 0.05$). In FI and FC, only a few new species were introduced, while mass-produced seeds of *S. borealis* germinated after the synchronized flowering, thereby causing an increase in abundance. Consequently, the direction of the vectors was toward NI, whereas FR and NR were toward the Ref.

In flowering stands (FR, FI, and FC), the coverage of the aboveground vegetation was greatly reduced due to dieback of *S. borealis* (Figure 5). Flowering and cutting, however, did not change the coverage of the plants with other growth forms significantly except for *S. borealis*, whereas rooting significantly increased those of the shrubs (F = 16.038, $p < 0.001$) and perennial herbs (F = 14.689, $p < 0.001$). However, that of the trees was not greatly increased. Some abundance of *S. borealis* was observed in the flowering stands even though the existing culms declined (Figure 5). That is because of the seedlings germinated and grown from mass-produced seeds. After 5 years, the coverage of the herbaceous stratum in FI stands was 10.5%. Of these, the coverage other than *S. borealis* was only 3.4%, whereas that of the *S. borealis* reached 7.1%.

Contrary to this, the high abundance of *S. borealis* in non-flowering stands with cutting (NC) or rooting (NR) was due to resprouting from underground of *S. borealis*. After the live culms were cut completely in the non-flowering stands (NC), the aboveground coverage restored to 45% in only one year and to 68% in 3 years. Cutting in non-flowering stands resprouted more *S. borealis* than rooting.

3.3. Regeneration of Tree Species

Flowering did not have significant effects on either richness or number of tree seedlings at least for five years (Table 3). Contrary to this, wild boar rooting had a significant effect, increasing the species richness of tree seedling (F = 23.106, $p < 0.001$, Table 3, Figure 6). Both variables increased significantly over time. The density of the tree seedlings was the highest in FR and the lowest in the Ref (Figure 6). Due to high variation among the stands, the tree seedling numbers was not significant for flowering, rooting, and cutting (Table 3).

Although the total number of tree species did not increase for flowering, the number of tree species yielding specific fruit types, e.g., samara, pome and drupe, and nut, greatly increased (for samara, F = 12.008, $p < 0.001$, for pome and drupe, F = 6.373, $p < 0.05$, and for nut, F = 5.227, $p < 0.05$). By rooting, the total number of tree species increased, and similar to flowering, the number of tree species yielding certain fruit types increased significantly (for samara, F = 7.993, $p < 0.05$, for pome and drupe, F = 11.203, $p < 0.001$, and for nut, F = 6.820, $p < 0.05$). The number of tree seedlings showed appreciable increase only in

species yielding fruits of pome and drupe type by flowering (F = 7.331, *p* < 0.001). The number of tree species and seedlings yielding fruits of the samara type was the highest. Among the species, *Fraxinus rhynchophylla*, *Acer pseudosieboldianum*, and *Acer pictum* var. *mono*, *F. rhynchophylla* were the most dominant. Next, the species yielding fruits of pome and drupe type were *Sorbus alnifolia*, *Prunus sargentii*, and *Cornus controversa*, while the species of nut type were *Quercus mongolica* and *Carpinus cordata*. All these species are major constituents of this forest. In particular, *Quercus mongolica* is the dominant canopy tree.
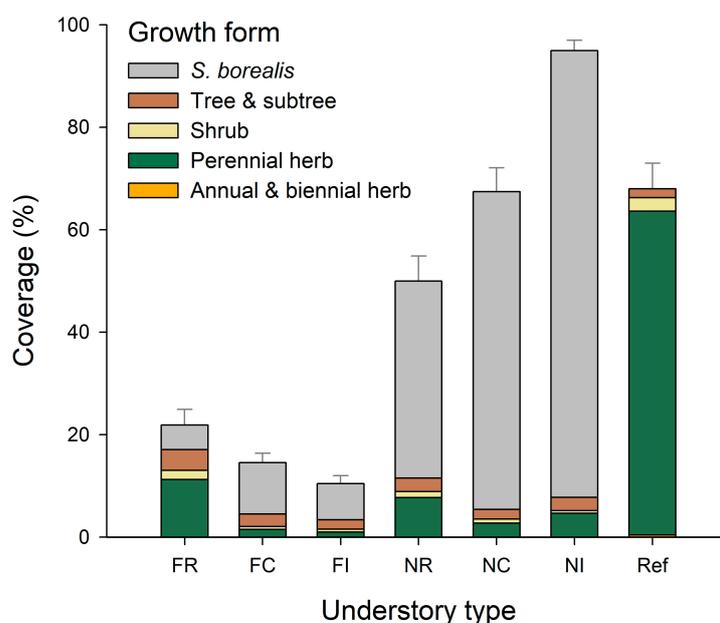
Figure 5. Vegetation coverage in the stands with seven understory types measured in 2020. The values are average ± standard error. FR: flowering and rooting, FC: flowering and cutting, FI: flowering and intactness, NR: non-flowering and rooting, NC: non-flowering and cutting, NI: non-flowering and intactness, Ref: reference.

Table 3. Repeated measures analysis of variance for the effects of flowering, rooting, and cutting on tree regeneration.

	Source	F-Value	*p*-Value
Tree seedling richness	Year	67.564	<0.001
	Year × Flowering	13.375	<0.001
	Year × Rooting	0.148	0.702
	Year × Cutting	1.510	0.224
	Year × Flowering × Rooting	5.670	<0.05
	Year × Flowering × Cutting	0.212	0.647
	Flowering	1.090	0.301
	Rooting	23.106	<0.001
	Cutting	0.945	0.335
	Flowering × Rooting	3.993	0.051
	Flowering × Cutting	0.747	0.391
No. of tree seedlings	Year	64.550	<0.001
	Year × Flowering	5.976	<0.05
	Year × Rooting	0.809	0.372
	Year × Cutting	1.046	0.311
	Year × Flowering × Rooting	0.280	0.599
	Year × Flowering × Cutting	0.312	0.579
	Flowering	2.625	0.111
	Rooting	1.768	0.189
	Cutting	0.577	0.451
	Flowering × Rooting	2.355	0.131
	Flowering × Cutting	0.652	0.423
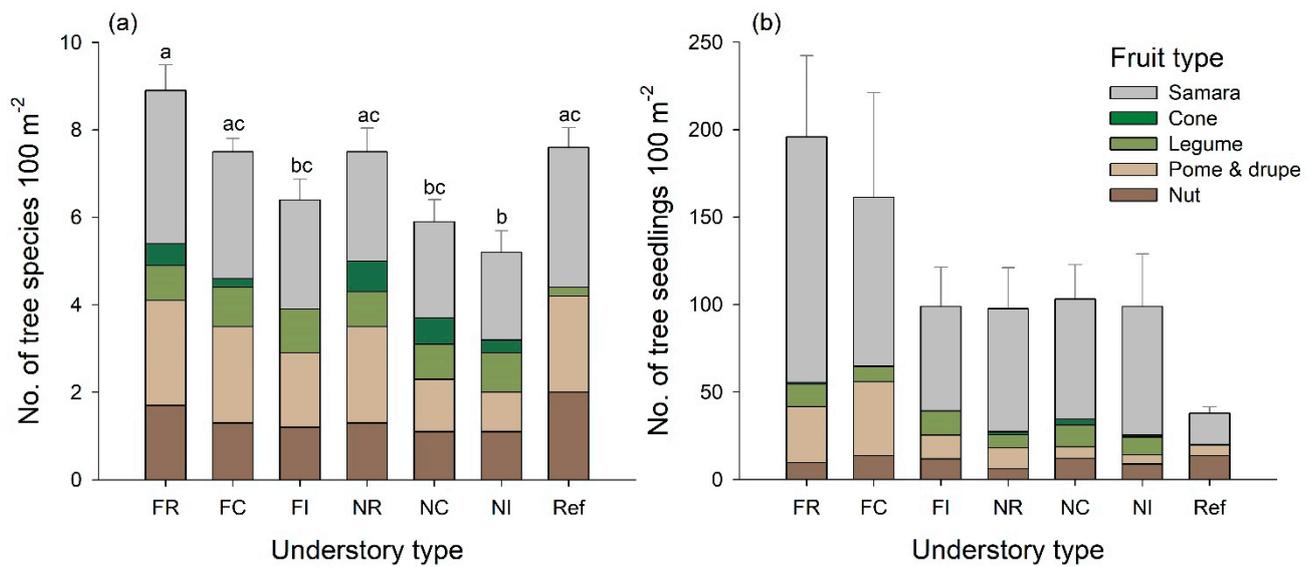
Figure 6. Tree regeneration in the stands with different understory types. (**a**) Tree seedling richness, and (**b**) number of tree seedlings in 2020. The values with different letters indicate significant difference at $p < 0.05$. The values are average ± standard error. FR: flowering and rooting, FC: flowering and cutting, FI: flowering and intactness, NR: non-flowering and rooting, NC: non-flowering and cutting, NI: non-flowering and intactness, Ref: reference.

3.4. Reestablishment of S. borealis

In flowering stands, it was found as a result of repeated measures ANOVA that with time the coverage of *S. borealis* seedling significantly increased (F = 18.860, $p < 0.001$), the height increased (F = 45.881, $p < 0.001$), while the density decreased (F = 31.284, $p < 0.001$) (Figure 7). Except for the year effect, the overall effects of rooting or cutting were not significant, nor was the interaction effect with year and other factors. However, in 2020, 5 years after flowering, the coverage of seedlings significantly decreased in FR, indicating the prominence of the rooting effect (Figure 7). The height and number of the seedlings were small in the FR stands in 2020; however, none of them were significant. Conversely, cutting had the opposite effect to that of rooting. That is, the coverage of *S. borealis* seedlings in FC was significantly higher than that of FR. Additionally, there was a higher number of taller seedlings even though the difference with FR was not significant.
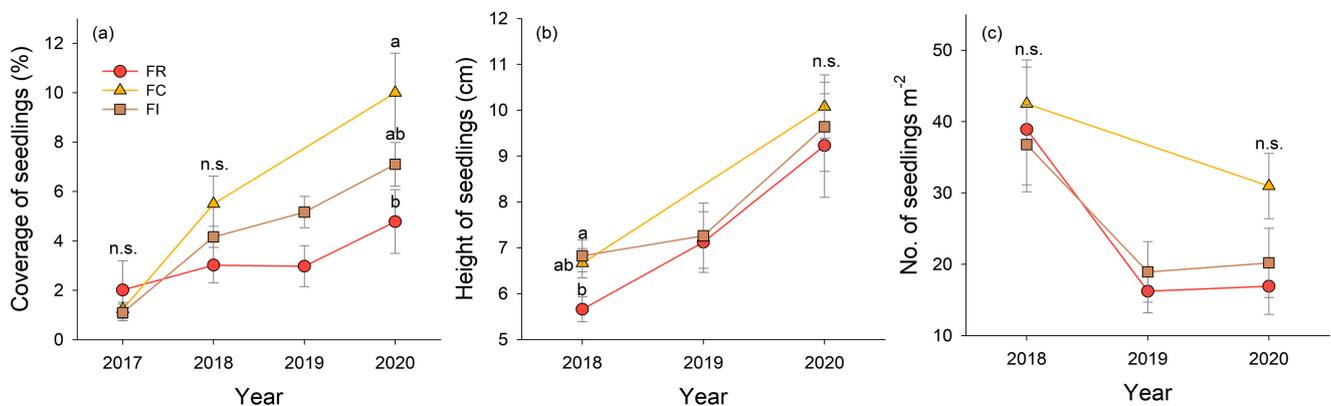
Figure 7. Reestablishment of *S. borealis* seedlings in flowering stands. (**a**) Coverage, (**b**) height, and (**c**) density. The values are average ± standard error. Difference between the three types was tested by ANOVA within a year except for 2019. The values with the different letters indicate significant difference at $p < 0.05$. n.s.: not significant. FR: flowering and rooting, FC: flowering and cutting, FI: flowering and intactness.

4. Discussion

We focused our interest on the very rare phenomenon of large-scale nationwide flowering of *S. borealis* in Korea [31] and studied its effect on subsequent forest regeneration. *Sasa* spp. are a typical species constituting the recalcitrant understory, but they have the monocarpic trait of synchronized dieback after synchronized flowering [31,49]. Therefore, we proposed the first hypothesis that such phenomena would help release the forests that had been suppressed by *S. borealis* and promote forest regeneration. There have been reports of positive regeneration of forests [3,47,48] due to improved light conditions [64,65], increased soil moisture, and soil nitrogen availability [5,66]. After thorough monitoring for 5 years after the dieback of *S. borealis*, we found the species diversity in the forests increased to a significant extent. However, it resulted from an increase in species evenness, not from any significant number of species recruitment. This means that an insignificant number of new species, including tree species, were introduced in the space where the environment changed.

This slow regeneration may be due to the effect of closed canopy, but more importantly, due to the remaining dead culms and underground mats. In particular, in the subterranean structure was observed a large-scale mat with densely intertwined rhizomes and roots at a depth of about 12–30 cm. Considering the densely entangled structure, mass, and chemical composition, it was estimated that a considerable amount of time will be required for the decomposition. Therefore, the surrounding vegetation is physically limited to expand and occupy new space. Makita [64] found that the number of dead culms decreased by 90% after 7 years of flowering for *S. kurilensis*. In this study, however, the richness did not increase even though the dead culms were removed, rather *S. borealis* was shown to resettle with time.

Our second hypothesis, that the rooting activity of wild boar will accelerate regeneration, is highly supported. Wild boar rooting contributed to the significant increase in the three species diversity indices independently without flowering. A higher number of tree species was included due to rooting, and the abundance of both shrub and herbaceous species increased significantly. Consequently, the species composition became similar to the reference stands. Furthermore, it suppressed the reestablishment of *S. borealis*. To search for diet, wild boars excavate the underground to the extent that mineral soil is exposed, significantly removing *S. borealis* [50].

In general, the effects of ungulates on forest regeneration, structure, and function have been reported negatively. Of the 433 papers, 70% reported negative impacts [67]. The abundance and richness of plants and animals decreased [68–71] and certain species, such as spring ephemerals, became vulnerable [72,73]. In the present study, it was found that wild boars actually play a positive role in forest regeneration by directly breaking the recalcitrant understory [74] and supplying seeds as disperser [75]. The supply of seeds to large areas where *S. borealis* has long monopolized would facilitate forest regeneration [76]. However, the activity of wild boar is unlikely to promote all species in an equal way. This is because ungulates, such as wild boars, act as ecological filters for plant species. Burrascano et al. [77] reported that plant species with different functional traits were selected according to the rooting intensity of wild boars. In addition, Alberts et al. [78] conducted a meta-analysis with 52 studies, revealing that ungulates differentiate the dispersal mechanisms of plant species. Our third hypothesis states that wild boars hindered the growth and reestablishment of *S. borealis*. Many monocarpic perennial plants mass-produce seeds after the synchronized flowering [65,79,80]. In fact, plenty of seedlings were observed to grow up to about 10 cm in height over 5 years and form a coverage of 7.3% in flowering stands, thereby showing the trend of reestablishment over time. In the rooted stands of wild boar, however, the coverage of *S. borealis* seedlings was significantly lower than those of the other understory types in 2020. Seedling density was also lower, although it was not significant.

The fourth hypothesis was that the removal of the culms will help the forest regenerate to some extent. Our results did not support this. One-time cut of the culms did not significantly affect any variables, such as species diversity and species abundance. After

the culms were cut in the non-flowering stands, the culms immediately resprouted and the aboveground coverage increased to three quarter of the non-flowering intact stands after 3 years. Even worse was that such cutting facilitated the seedlings of *S. borealis* to reestablish. There have been several attempts to control *Sasa* spp. For three years, Kim [43] removed the culms of *S. quelpaertensis* which dominated the Jeju Island, and found the culm size decreased. Kudo et al. [44] found that species richness only returned to pre-*Sasa* levels after 7 years of annual removal of *S. kurilensis*. This emphasized that years of effort are required for full recovery.

On the other hand, Masaki et al. [27] did not succeed to remove *S. palmata* and *S. kurilensis* in spite of 10 years of repeated weeding and herbicide use. This may be due to physiological integration with the surrounding containing undamaged *Sasa* [25]. Similar to our results, there are arguments that removal of the live culms rather promotes the production of new culms [27,81–83]. On the other hand, there were studies that soil scarification, which displaced surface soil with machinery such as bulldozers, was effective in removing dwarf bamboo in northern Japan [84]. For silvicultural site preparation, it can be applied to a certain area. However, it is considered that serious side effects such as soil erosion will follow if it is applied to natural forests developed in large areas and sloping mountain areas. Therefore, there seems to be no applicable method to effectively remove *Sasa* spp.

Overall, dieback after flowering of *S. borealis* was an opportunity to regenerate the suppressed understory of the forest to some extent [3,16,47]. Nevertheless, after five years, the regeneration with flowering is still in its early stage. Such regeneration was limited to increase in species diversity driven by increase in species evenness and increased in some type of tree species with the samara, pome and drupe, and nut. Understory gaps were created by dieback, but the canopy was still almost closed, so the flowering effect seemed to be slow. To promote rapid regeneration of the forest, it seems that canopy gaps are also necessary [47].

Meanwhile, mass-produced seeds of *S. borealis* germinated, and the seedling abundance was increasing significantly with time. There is a high probability that *S. borealis* will take over the available space again in some flowering stands. The faster the reestablishment of *Sasa*, the more difficult it would be for other plants to settle. Sakurai [85] found that *S. ishizuchiana* recovered to its pre-flowering biomass in open area within 10 years. Similarly, Makita [64] also found that *S. kurilensis* recovered to 84% of its pre-level in 10 years after flowering, while the coverage of other plants was only 4% in closed *Betula ermanii* forest. The recovery of *S. kurilensis* was faster in forests with good light conditions [86,87].

In the stands where the aboveground declined, wild boar's impact was enormous. It promoted forest regeneration by increasing species richness, while it inhibited re-occupancy of *S. borealis*. Wild boar removed the leftover tightly bound structures of the underground together with the aboveground. This is an obvious synergistic effect of the dieback of *S. borealis* and wild boar activity. Consequently, the recalcitrant understory formed by *S. borealis* was broken.

Populations of wild boar, as high reproductive omnivores, are increasing worldwide including in Korea due to the absence of predators, increased winter temperature, reduced snowfall, and increased *Quercus* forests [50,88–90]. Traces of wild boar were very frequently found in forests [50]. This suggests that the synergistic effect can effectively act on forest regeneration. However, although the number of wild boars is increasing, the rooting area is small. Therefore, at landscape scale, the synergistic result is to split the large *S. borealis* dieback areas into patches of various sizes and mosaic them. In areas with only dieback without wild boar activity, *S. borealis* tended to reoccupy faster, while the other plants were restoring slower. Therefore, long-term monitoring is necessary to gain a clearer view of forest regeneration following synchronized flowering.

5. Conclusions

Monocarpic dwarf bamboo, *S. borealis* is one of the species that arrests forest development by constituting a recalcitrant understory under closed forests. It reduces species diversity and suppresses regeneration of other plants during a long vegetative period, estimated to be several decades. However, a very rare event of synchronized flowering and thereafter dieback occurred around 2015, so we were expecting an opportunity for the forests to regenerate. We focused on comparison between permanent plots established after mass flowering. Species diversity increased 5 years after dieback, including increase of some types of tree species, but simultaneously, *S. borealis* also showed signs of reestablishment.

The synergistic effect of rooting activity and flowering was remarkable. The wild boar physically broke the structure of the recalcitrant understory by removing both the culms and underground mats. This increased significantly the abundance of perennial herbs and shrubs, and number of new species, including tree species yielding fruits of the samara, drupe and pome, and nut type. This led to changes in the species composition in flowering and rooted stands to a direction similar to that of the surrounding reference forest. On the other hand, this blocked the reestablishment of *S. borealis* significantly. The effect of culm cutting was not positive. It rather increased the likelihood of *S. borealis* resettling in the flowering stands, and promoted resprouting in the non-flowering stands.

Overall, we found the sign of forest regeneration due to the synchronized dieback of *S. borealis*. Furthermore, when wild boar activity was combined with the dieback, the synergistic effect on forest regeneration was outstanding. At landscape scale, considering several factors such as flowering and non-flowering, the prevailing activity of wild boar, and an increase in their population size, the forests which have been long suppressed by *S. borealis* are projected to regenerate with mosaic forests.

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