

# Species richness of the understory woody vegetation in Japanese cedar plantations declines with increasing number of rotations

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**Abstract** The possibility of restoring natural broadleaf forests may be decreased by the effects of plantation management, particularly in sites that undergo repeated rotation. We investigated the following two working hypotheses about the effects of repeated plantation of conifers on the natural regeneration of woody saplings in cool-temperate Japanese cedar plantations: (1) that repeated plantation of conifers decreases sapling species richness, and (2) that repeated plantation of conifers changes sapling species compositions. Our result supported the first hypothesis, because species richness was significantly lower in second-rotation plantations than in first-rotation plantations. The second hypothesis was not supported, because no significant or substantial differences in species composition were observed between plantations with different numbers of rotations. However, the abundance of tree (nonshrub) and gravity-dispersed species decreased after the second rotation of large saplings, albeit not those of small saplings, suggesting that response to repeated rotation depended on sapling size. Our results suggest that it is important to consider factors affecting the maintenance of a species in the plantations, such as distance from natural forests and seed sources, to minimize the effects of repeated plantation.

**Keywords** Growth form · Light environment · Seed dispersal · Seed source · Species composition

## Introduction

Planted forest area has been increasing worldwide, but the negative effect of planted forests on biodiversity is a concern because of their simple species compositions and even-aged structures (Brockerhoff et al. 2008; Bremer and Farley 2010). The global total planted forest area has been increasing at a rate of 5 million hectares per year since 2005, and reached 7 % of the total forested area in 2010 (FAO 2010). The area of planted conifer forest in Japan currently exceeds 100,000 km<sup>2</sup> (42 % of the forested area) and 27 % of the total land area (Japan Forestry Agency 2011) because of afforestation after WWII. This increase in planted area could be causing losses of wildlife habitat and degrading forest ecosystems.

Natural forests have recently been rehabilitated, and attempts have been made to restore biodiversity by converting coniferous monocultures into broadleaf or mixed forests in Europe and Japan (Yamagawa et al. 2010; Brown et al. 2015). Species richness and the composition of advanced broadleaf tree seedlings in planted forests will play important roles in this scenario (Yamagawa et al. 2007). Species richness and the composition of advanced broadleaf woody seedlings are mainly affected by the understory environment, distance from the seed source, and the seed dispersal attributes of the species (Yamagawa et al. 2007; Gonzales and Nakashizuka 2010). In particular, when plantation management is repeated at a single site, the possibility of natural forest restoration is expected to decrease; however, information about repeated plantation remains limited.

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Many of the present coniferous plantations in Japan are first-generation plantations, implying that they were established after the clear cutting of natural broadleaf forests (Miyamoto et al. 2011). Most of these plantations will be replaced with conifer plantations after future harvests, resulting in an increase in the number of subsequent-generation plantations (Nagaike 2012). Some effects of repeated plantation on advanced seedlings have been reported. First, advanced seedling species richness decreases with increasing number of plantation rotations because the forest structure is simplified, e.g., through soil acidification due to litter fall (Takafumi and Hiura 2009). In contrast, understory plant species richness increases with increasing number of rotations (Jeffries et al. 2010), or the species richness of understory woody vegetation does not change (Ito et al. 2003). Second, species composition changes such that species with particular traits dominate (e.g., early-seral species, Jeffries et al. 2010). This may be caused by the accumulating effect of plantation management. However, the number of late-seral species increases in response to repeated plantation (Nagaike et al. 2012). Another example is that second-rotation Japanese cedar plantations have higher shrub and bird-dispersed species richness than first-rotation plantations do (Ito et al. 2003). This may be caused by differences in re-establishment ability among seed dispersal types and the selective elimination of woody species by management. However, opposite results have been reported; for example, the number of tree (nonshrub) species and wind-dispersed species increase in response to repeated plantation (Nagaike et al. 2012). These conflicting results may be partly due to differences in the stand ages of the studied plots. Most previous studies have included plantations at different developmental stages to estimate the general effect of repeated plantation (Ito et al. 2003; Takafumi and Hiura 2009; Nagaike et al. 2012). Additionally, different forest management histories due to differences in ownership are also expected to affect the species richnesses and compositions of plantation forests. Thus, the effects of repeated plantation are more accurately determined by selecting survey stands that are similar in stand age and ownership, and by reducing variations in soil or topographic conditions that could blur the effects of the number of rotations.

Our aim in this study was to evaluate the effects of repeated plantation more clearly by limiting the survey stands to only mature plantations ~40–50 years in age that belong to the national forest and have similar understory vegetation coverages. We tested two working hypotheses about the effect of repeated conifer plantation on advanced seedlings in a cool-temperate forest zone: (1) that repeated conifer plantation decreases advanced seedling species richness, and (2) that repeated conifer plantation changes the species composition of advanced seedlings by

decreasing particular species, such as woody species, that are less competitive with planted trees or species with low dispersal ability.

## Materials and methods

### Research stands

Our research stands were located in the Ogawa Forest Reserve (36° 56'N, 140° 35'E) at the southern edge of the Abukuma Mountains, central Japan (Masaki et al. 1992). The elevations of the research stands were 500–750 m above sea level. The mean annual temperature at Ogawa Forest Reserve where the elevation is ~650 m is 10.7 °C (range –0.9 °C in January to 22.6 °C in August) (Mizoguchi et al. 2002). The mean annual precipitation is 1910 mm, of which more than half falls during the growing season (Mizoguchi et al. 2002). The bedrock is granite and the major soil type is Cambisol (Yoshinaga et al. 2002).

Old-growth natural forests in this area mainly consist of *Fagus*, *Quercus*, *Carpinus*, and *Acer* species (Masaki et al. 1992). Secondary forests that developed from abandoned pasture or coppice forests and coniferous plantations are the dominant landscape components in this area, with a few small and fragmented old-growth forests remaining (Suzuki 2002).

Twelve plantations of Japanese cedar (*Cryptomeria japonica* D. Don) were selected as research stands (Table 1). All stands belonged to the Japanese National Forest, and the management histories of the stands were similar (weeding 4–6 times, improvement cutting 1–2 times, and thinning 1–2 times). The stand areas were 5–37 ha and the ages were 38–51 years. We defined a first-rotation plantation as a plantation that was established after clearcutting the natural broadleaf forest, and a second-rotation plantation as a plantation established after clearcutting a first-rotation plantation. The previous land uses at each site were determined from old forest inventory records. The ages of the previous natural forests when the first-rotation plantations were established were unknown, but the ages of the plantations when the second-rotation plantations were established were estimated to be 40–50 years based on the standard harvest age of plantations around the survey area. Among the 12 stands, six were first-rotation plantations (FP1–FP6) and the other six were second-rotation plantations (SP1–SP6). These stands were selected to cover a similar range of stand ages, slopes, bedrock types, and soil types. The stands almost had a closed canopy, and no conspicuous gaps were observed. The stands were at least 1 km from each other. Therefore, bias resulting from spatial autocorrelation caused by local species dispersal was negligible in this study.

**Table 1** Main characteristics of the 18 study stands

Stand	Age	Area (ha)	Canopy height (m)	Aspect	Slope	Bedrock	Soil type
FP1	38	17	13	North	Moderate	Granite	Cambisol, Eutic
FP2	50	9	19	West	Moderate	Crystalline schist	Cambisol, Eutic
FP3	48	31	14	Northeast	Moderate	Granite	Cambisol, Eutic
FP4	44	9	15	East	Moderate	Granite	Cambisol, Eutic
FP5	40	17	15	West	Moderate	Granite	Cambisol, Eutic
FP6	43	5	16	West	Moderate	Granite	Cambisol, Eutic
SP1	43	24	16	Northeast	Steep	Granite	Cambisol, Eutic
SP2	47	37	18	North	Moderate	Granite	Cambisol, Eutic
SP3	43	11	17	North	Moderate	Granite	Cambisol, Eutic
SP4	38	6	15	Southeast	Moderate	Granite	Andosol
SP5	38	9	13	Southwest	Moderate	Granite	Cambisol, Eutic
SP6	51	7	16	East	Moderate	Granite	Cambisol, Eutic
BL1	>100				Moderate		
BL2	>100				Moderate		
BL3	47	4		Southwest	Moderate	Granite	Andosol
BL4	>100	33		Southeast	Moderate	Granite	Cambisol, Eutic
BL5	>100	9		North	Steep	Granite	Cambisol, Eutic
BL6	>100	12		East	Steep	Granite	Cambisol, Eutic

Moderate and steep slopes correspond to 20–30° and >30°, respectively

Soil types are defined according to FAO

FP first-rotation Japanese cedar plantation, SP second-rotation Japanese cedar plantation, BL broadleaf natural forest

In addition, six natural broadleaf forest stands were selected as controls. The natural broadleaf forest stands included one 47-year-old secondary forest, three secondary forests that were >100 years old, and two old secondary forests for which no age records were available. The last two forests appeared to be >100 years old based on forest physiognomy.

**Field methods**

We established a 10 m × 100 m study plot at the center of each stand to investigate the distribution of broadleaf woody saplings during summer 2004. The plots were oriented with the long side along a contour to minimize the effect of topographic variations in each stand (Iida and Nakashizuka 1995; Fukamachi et al. 1996; Nagaike 2002; Nagaike et al. 2006). Each plot was divided into 5 m × 5 m subplots (n = 40), and a 1 × 1 m<sup>2</sup> quadrat was established on the outer edge within each subplot.

We divided the saplings into two size categories: large saplings [height >2 m and diameter at breast height (DBH) <5 cm], and small saplings (5 cm <height ≤2 m). Large saplings were considered older, whereas the small saplings were considered relatively newer recruits. Thus, we evaluated the condition of each plantation roughly in terms of sapling age by separately analyzing the distributions of large and small saplings. Presence/absence of large sapling

species was investigated in each subplot and that of small sapling species in each quadrat. We tested the correlation between the number of quadrats/subplots where a woody species was present and the number of individuals using data from Masaki et al. (2004), who performed a similar study, and confirmed that there were highly significant correlations (r = 0.86 for large saplings and r = 0.82 for small saplings) between them. We used the number of quadrats as a substitute for abundance. Trees (height >2 m and DBH >5 cm) were identified and tagged, and their DBHs in each subplot were measured. In total, 101 woody plant species were observed (see the Appendix). We classified the growth forms of the woody species found at our study sites into trees and shrubs based on the descriptions given in several works in the literature (Kitamura and Okamoto 1959; Kitamura et al. 1974, 1978; Kitamura and Murata 1980). Seed dispersal types were classified on the basis of seed or fruit morphology, as illustrated in the above literature, into wind-dispersed, bird-dispersed (e.g., fleshy berries), and gravity-dispersed (no specialized dispersal mechanism).

The mean height of the canopy trees was used as the stand height. Coverage (%) of dwarf bamboo species (*Arundinaria ramosa*, *Sasamorpha borealis*, and *Sasa nipponica*), which inhibit the regeneration of woody seedlings (Ito and Hino 2007), was assessed visually in each quadrat. Hemispherical photographs were taken 1 m

above each quadrat to estimate the forest-floor light environment (also in each subplot) using a Nikon Coolpix 4500 digital camera equipped with a Nikon FC-E8 fisheye lens (Nikon Inc., Tokyo, Japan). Openness of the canopy was evaluated by analyzing the photographs using Gap Light Analyzer 2.0 (Frazer et al. 1999).

## Analysis

We examined woody species richness (number of species) in each quadrat (small saplings) or subplot (large saplings) in relation to the number of plantation rotations and stand and landscape structural parameters using a generalized linear mixed model (GLMM), with the log link function and a Poisson distribution. In addition to the number of rotations, we used stand-level variables such as stand age (years) and stand height (m), and subplot (quadrat) level variables such as basal area of the canopy trees (DBH >5 cm), canopy openness (%), and coverage of dwarf bamboo species (%) (Table 2). In addition, the proportion of natural forest, calculated as the proportion of natural forest within a 100-, 200-, or 300-m radius from the center of each plot (R100, R200, and R300, respectively) were added as additional stand-level variables as indices of potential seed immigration density. Stand identity was considered a random factor. Table 2 summarizes the range of values for the explanatory variables. Multicollinearity between variables was examined, and variables with high correlations were not included in the same model. The model was selected on the basis of Akaike's information criterion (AIC). AIC values were compared for all possible models, and the model with the lowest AIC was selected as the best.

We assessed the differences in small and large sapling composition between stands by nonmetric multidimensional

scaling (NMDS). NMDS is an ordination method that provides views of a high-dimensional space by displaying the structure using lower-dimensional plots. In this study, the distribution of stands in the  $n$ -dimensional species space (where  $n$  equals the number of species observed) was projected as a two-dimensional plot. The Sørensen dissimilarity measure (McCune et al. 2002) was used to indicate compositional dissimilarity between stands, which was estimated on the basis of the abundance (number of quadrats or subplots) of each species.

We used multi-response permutation procedures (MRPP) to test for differences in woody species composition between forest types. MRPP is a nonparametric procedure that is used to test the hypothesis of no difference between groups of multivariate data (McCune et al. 2002). The distance measure in this analysis was Sørensen's dissimilarity measure.

We compared the abundance of each growth form and seed dispersal type between forest types to assess the sensitivity of each type to the number of rotations. The abundance of each species in each growth form or seed dispersal type was summed over species and plots, and the comparison was executed using the  $\chi^2$  test and an analysis of residuals.

We grouped species based on occurrence between the first and second rotations to examine the shared species between rotations. The groups were defined as “first-only species,” which appeared only at the first rotation, “shared species,” which appeared at both rotations, and “second-only species,” which appeared only at the second rotation. We compared the abundance and species richness of different life-history traits such as each growth form and seed dispersal type between these groups.

**Table 2** Explanatory variables used in the GLMM analysis and their values in the first- and second-rotation Japanese cedar plantations

Explanatory variables	Abbreviation	First rotation			Second rotation		
		Min	Median	Max	Min	Median	Max
Stand-level variables							
Number of rotations	ROTATION	1	1	1	2	2	2
Stand age (years)	AGE	38	44	50	38	43	51
Stand area (ha)	AREA	5	13	31	6	10	37
Height (m)	HEIGHT	13	15	19	13	16	18
Proportion of natural forests within (%):							
100 m	R100	0	0	18	0	0	23
200 m	R200	0	3	24	1	1	22
300 m	R300	0	6	22	2	15	24
Subplot-level variables							
Basal area of canopy trees (m <sup>2</sup> ha <sup>-1</sup> )	BA	0	28	77	0	32	91
Coverage of dwarf bamboo (%)	SASA	0	0	63	0	0	38
Canopy openness (%)	LIGHT	6	10	14	7	10	11

**Table 3** Mean species richness and abundance of each growth form and of each dispersal type of woody plant

	Small saplings			Large saplings		
	First	Second	<i>p</i>	First	Second	<i>p</i>
Species richness	1.3	0.7	<0.01	2.2	1.2	<0.01
Growth form			0.56			<0.01
Shrub	242	126		211	(–) 226	(+)
Tree	104	47		545	(+) 301	(–)
Dispersal type			0.62			<0.01
Bird	226	117		488	(–) 420	(+)
Gravity	104	51		159	(+) 40	(–)
Wind	16	5		109	67	

The number of quadrats (for small saplings) or subplots (for large saplings) where a species occurred was used as a substitute for the abundance of that species

Significance levels of  $\chi^2$  tests are indicated by *p* values

Values in parentheses are significantly lower (–) or higher (+) than the expected value based on  $\chi^2$  tests with analysis of residuals (*p* < 0.05)

All analyses were performed using the R software ver. 2.12.1 (R Development Core Team 2016) with the vegan package (Oksanen et al. 2016).

**Results**

**Species richness**

No significant random stand effect was detected in either model. The mean small and large sapling species richness in all quadrats of the first-rotation plantations was significantly higher than that in the second-rotation plantations (*t* tests, both *p* < 0.05; Table 3).

**Factors affecting species richness**

The small sapling model with the lowest AIC included three significant variables (Table 4): stand area (AREA), number of rotations (ROTATION), and proportion of natural forest within 300 m (R300). In this model, species richness was negatively affected by ROTATION (lower in second-rotation) and AREA but positively affected by R300.

The large sapling model with the lowest AIC included AGE and R100 (Table 4) and one marginally significant variable (ROTATION). In this model, AGE and R100 positively affected species richness, whereas ROTATION negatively affected species richness (lower in the second rotation).

**Species composition**

The dominant broadleaf forest species were the large saplings of *Carpinus cordata* and *Acer palmatum* var.

**Table 4** Small and large woody plant sapling species richness as a function of stand attributes (GLMM analysis)

	Estimate	Std. error	Z value	Pr (> z )	Sig. level
<b>Small saplings</b>					
(Intercept)	–2.043	0.908	–2.250	0.024	*
AREA	–0.065	0.015	–4.431	<0.001	***
ROTATION	–0.861	0.198	–4.351	<0.001	***
R300	0.049	0.013	3.858	<0.001	***
<b>Large saplings</b>					
(Intercept)	–7.133	2.581	–2.764	0.006	**
AGE	0.167	0.057	2.933	0.003	**
BA	0.003	0.002	1.409	0.159	
ROTATION	–0.768	0.428	–1.794	0.073	
R100	0.083	0.032	2.585	0.010	**

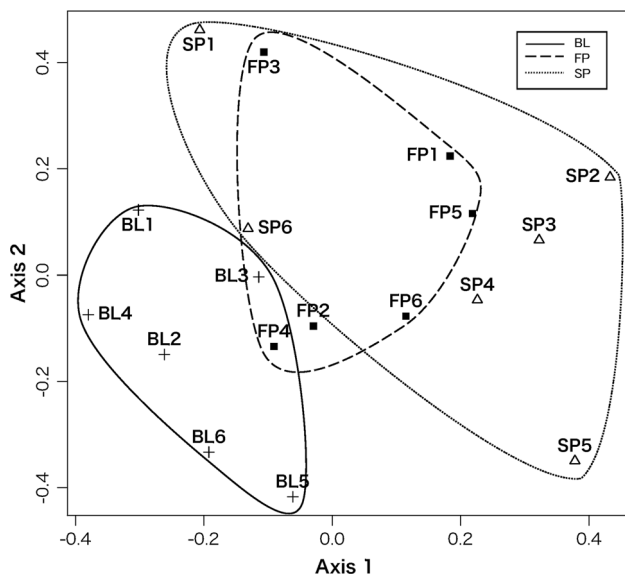
Values are coefficients and statistics for the model with the best fit based on Akaike’s information criterion (AIC). Abbreviations for the parameter names are defined in Table 2

Sig. levels \*\*\* *p* < 0.001, \*\* *p* < 0.01, \* *p* < 0.05, *p* < 0.1

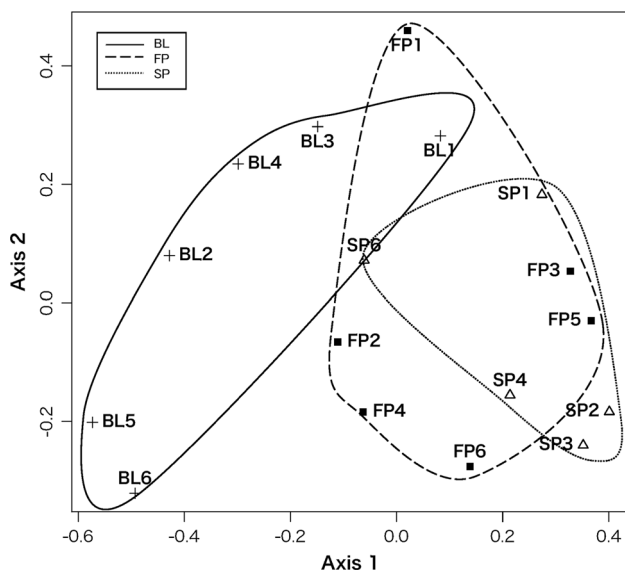
*amoenum* and the small saplings of *Viburnum dilatatum* and *A. palmatum* var. *amoenum*. Dominant species in the first-rotation plantations were the large saplings of *Padus grayana* and *Callicarpa japonica* and the small saplings of *Rubus palmatus* and *Clethra barbinervis*. Dominant species in the second-rotation plantations were the large saplings of *Parabenzoin praecox* and the small saplings of *Callicarpa japonica*, *Rubus palmatus*, and *Hydrangea involucrata* (Appendix). The first- and second-rotation plantations overlapped largely in the NMDS ordination for the small and large saplings (Figs. 1, 2). In contrast, broadleaf forests were mostly segregated from the plantations.

The MRPP analyses also showed that small (*p* = 0.69) and large (*p* = 0.66) sapling species compositions did not differ significantly between the first- and second-rotation





**Fig. 1** Results of the non-metric multidimensional scaling (NMDS) ordination for small woody plant species (small saplings). *BL* broadleaf forest (crosses, enclosed by a solid line), *FP* first-rotation plantation (black squares, enclosed by a broken line), *SP* second-rotation forest (white triangles, enclosed by a dotted line)



**Fig. 2** Results of the non-metric multidimensional scaling (NMDS) ordination for large woody plant species (large saplings). *BL* broadleaf forest (crosses, enclosed by solid line), *FP* first-rotation plantation (black squares, enclosed by a broken line), *SP* second-rotation forest (white triangles, enclosed by a dotted line). Stand SP5 was omitted from this ordination because too few large saplings were observed

plantations (Table 5). In contrast, the species compositions of small and large saplings differed substantially between the plantations and natural broadleaf forests ( $p = 0.01\text{--}0.06$ ) (Table 5).

## Species traits

No difference in the growth form composition of small saplings was detected between the first- and second-rotation plantations (Table 3). A significant difference was detected for large saplings, but the relative proportions were significantly lower for tree species and significantly higher for shrub species in the second-rotation plantations than for the first-rotation plantations.

No differences in dispersal type were observed between the first- and second-rotation plantations for small saplings (Table 3). A significant difference was observed for large saplings, but the relative proportions were significantly lower for gravity-dispersed species and significantly higher for bird-dispersed species in the second-rotation plantations than for the first-rotation plantations (Table 3).

## Characteristics of shared species in the repeated plantations

Twenty-three small sapling species appeared only in the first rotation (first-only species), 36 species were shared (shared species), and 10 species appeared only in the second rotation (second-only species) (Table 6). The numbers of first-only, shared, and second-only large sapling species were 29, 43, and 8, respectively. The proportion of shared species was significantly higher in the species groups with a higher abundance in the first-rotation plantations for small- ( $\chi^2$  test,  $p = 0.02$ ) and large-sized ( $\chi^2$  test,  $p < 0.01$ ) saplings (Fig. 3). The life-history traits of the first-only, shared, and second-only species indicated no significant difference in relative species richness of large saplings (Table 6). In contrast, for small saplings, a marginally significant difference was detected, where shared species showed a higher proportion of bird-dispersed species and a lower proportion of wind-dispersed species.

## Discussion

Our first hypothesis, that repeated rotation decreases species richness, was supported by our results. Species richness was significantly lower in second rotations than in first rotations for both small and large saplings (Table 3). The GLMM results also showed that ROTATION negatively affected species richness (lower in second rotations) for small and large saplings (Table 4). These results may have been caused by the accumulation of negative effects from plantation forestry. Plantations are usually similarly aged monocultures after clearcutting, which creates a homogeneous forest floor (Turner et al. 1998). An even-aged monoculture results in a simple canopy structure and a simple forest floor light environment (Ishii et al. 2004;

**Table 5** Comparisons of species composition performed using a multi-response permutation procedure (MRPP) analysis among the first-rotation plantations, second-rotation plantations, and natural broadleaf forests

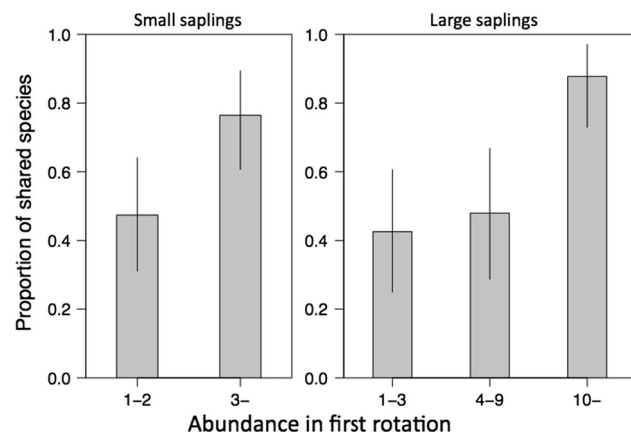
	First-rotation plantations	Second-rotation plantations	Natural broadleaf forests
First-rotation plantations	–	0.66	0.02
Second-rotation plantations	0.69	–	0.01
Natural broadleaf forests	0.06	0.01	–

Each number in the table represents a significance level (*p* value). Species compositions differed significantly if the *p* value was <0.05  
*p* values for comparisons of large saplings are shown in the upper right part of the table, and those for comparisons of small saplings are shown in the lower left part

**Table 6** Comparisons of woody plant species richness among those appearing only in the first-rotation (F), shared by both rotations (Sh), and appearing only in the second rotation (S) with reference to the different growth forms and seed dispersal types

	Small saplings				Large saplings			
	F	Sh	S	<i>p</i>	F	Sh	S	<i>p</i>
Total	23	36	10		29	43	8	
Growth form				0.44				0.19
Shrub	11	19	3		12	13	5	
Tree	12	17	7		17	30	3	
Dispersal type				0.08				0.46
Bird	9	25 (+)	4		11	24	4	
Gravity	8	9	3		11	8	2	
Wind	6	2 (–)	3		7	11	2	

Significance levels of *t* tests and  $\chi^2$  tests are indicated by *p* values. Values in parentheses are significantly lower (–) or higher (+) than the expected value based on  $\chi^2$  tests with analysis of residuals (*p* < 0.05)



**Fig. 3** Proportion of species shared between the first- and second-rotation plantations as a function of abundance in the first-rotation plantations. For each abundance class, the proportion of shared species was calculated as the number of species observed in the first- and second-rotation plantations divided by the number of species in the first-rotation plantations. Each abundance class included about 25 species. Error bars indicate 95 % confidence intervals. *P* value of  $\chi^2$  test was 0.02 for small saplings and <0.01 for large saplings

Kelty 2006). In addition, the rotation period of a plantation is usually shorter than the canopy turnover in a natural forest. Rotation periods of natural forests in Japan are usually more than 100 years old (Tanaka and Nakashizuka 1997), and the regular rotation period of a plantation is ~50 years. A short rotation period would result in less time for species diversity to recover under plantation conditions (Ito et al. 2003).

The decrease in species richness observed after repeated plantation has been reported in *Larix*, *Abies*, and *Picea* plantations in the cool-temperate region of Hokkaido (Takafumi and Hiura 2009), but not in a Japanese cedar plantation in Kyushu, which is in a warm-temperate region (Ito et al. 2003). This difference may be caused by different sapling leaf phenologies (deciduous vs. evergreen) in different climates. Our study was performed in a cool-temperate region, and the natural forests were originally composed of deciduous species, as in the natural Hokkaido forests (Takafumi and Hiura 2009). In contrast, natural forests in Kyushu consist of many evergreen species (Ito et al. 2003). Generally, evergreen woody species are expected to be more shade tolerant than deciduous woody species, and more capable of surviving as advanced seedlings under a canopy (Niinemets and Valladares 2006). This might explain the discrepancy between the results presented here and for Hokkaido and those for Kyushu forests.

The factors affecting species richness other than the number of rotations differed between small and large saplings (Table 4). Small sapling species richness was negatively affected by AREA (stand size) but positively affected by R300 (proportion of natural forest within 300 m). These factors may explain the negative effect of seed dispersal limitation on species richness. A large stand resulting in a smaller proportion of natural forest around a plot could decrease seed input from nearby forests. In contrast, R300 could increase seed input. For large saplings, AGE and R100 positively affected species richness. Species richness of large saplings could increase with age during transition from small saplings. Although we

sampled similarly aged plantations (38–51 years), stand age was a significant factor. Previous studies (Ito et al. 2003; Takafumi and Hiura 2009; Jeffries et al. 2010) reported different results for repeated plantations because the ages of their stands varied more than they did in this study. In this study, the value of AGE might merely reflect duration of sapling height growth after thinning. We also found that the proportion of natural forest around a stand (R100) positively affected large sapling species richness as well as small saplings (R300). The species richness of large saplings was affected by seed source at a shorter distance than small saplings. On the other hand, species richness of tree species and wind-dispersed species were higher in large saplings than in small saplings (Table 6), and the main component of wind-dispersed tree species was *Acer* species (Appendix). Accordingly, the shorter dispersal distance at large saplings may be caused by the relatively short dispersal distance and higher shade tolerance of *Acer* species (Nakashizuka et al. 1995). These factors should be considered when studying the relationship between species richness and the number of rotations. Additionally, if necessary, forest ownership should be included as a factor to avoid elucidating incorrect conclusions.

No differences in species composition were observed on the basis of the number of rotations (Table 5; Figs. 1, 2). Therefore, our second hypothesis was not supported. In addition, no differences in growth form or seed dispersal type composition were observed for small saplings between rotations (Fig. 1; Tables 3, 5). On the other hand, we observed lower abundances of tree (non-shrub) species and gravity-dispersed species at the second rotation for large saplings. We also found that the abundances of shrub species and bird-dispersed species were higher at the second rotation for large saplings (Table 3). For small saplings, species richness was significantly higher for bird-dispersed species and lower for wind-dispersed species at shared species rather than at first-only or second-only species (Table 6). This means that bird-dispersed species were less sensitive to the repeated plantation than wind-dispersed species. This may be due to the higher dispersal ability of birds than the wind. However, these differences did not affect total species composition, as stated above. One possible reason is that understory woody vegetation in a mature first-rotation plantation may have already changed distinctly from that of a natural forest. In this case, species vulnerable to plantation management became locally extinct after clearcutting the broadleaf forest and managing the first-rotation plantation. In this study, the dominant plantation species were disturbance-tolerant species, such as *Clethra barbinervis*, *Rubus palmatus*, *Hydrangea involucrata*, *Padus grayana*, and *Callicarpa japonica* (Appendix). The dominant species were common (*R. palmatus* for small saplings and *C. japonica* for large saplings)

to the first- and second-rotation plantations. In contrast, the dominant broadleaf forest species were mainly shade-tolerant species, such as *Acer palmatum* var. *amoenum* and *Carpinus cordata*, which were different from the plantation species. Therefore, species in mature plantations may be primarily plantation- and disturbance-tolerant species that are less sensitive to repeated plantation management. Our results showed that species richness decreased with repeated rotations and that species composition did not change between rotations, which seems to be contradictory. This reflected that repeated plantation did not affect the occurrence of the more abundant species but did negatively affect the occurrence of minor species. Our results support this speculation (Fig. 3). Thus, some species with low abundances may have been eliminated by chance with the rotations, which would decrease species richness. Species composition was unaffected as a whole because highly abundant species were seldom lost by this mechanism. Therefore, it is necessary to consider the negative effects of repeated plantation, particularly on the occurrence of rare species, even when no drastic change in species composition is detected.

However, the results of our study should be interpreted carefully. For example, species composition is expected to depend on pre-management site-specific conditions, such as logging or thinning. Unfortunately, in our study, we have no data about the pre-management conditions. Monitoring the stands before and after management is necessary to make the study more robust.

In conclusion, species richness and some species traits were affected by repeated plantation, although community structure in the plantations, which differ considerably from natural forests, was almost unaffected except for decreases in the abundances of relatively rare species. It is important to consider factors affecting the maintenance of a species in the plantations, such as distance from natural forests and seed sources, when attempting to control the negative impacts of repeated plantation on species diversity in plantations.

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