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ORIGINAL PAPER

The effects of patch age and edges on understory tree distribution in an uneven-aged conifer plantation formed by small-scale clearcutting

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Abstract
We verified whether broadleaf tree populations in the understory of an uneven-aged conifer plantation followed Oliver's model of natural forest recovery, and examined the contribution of forest edges between patches of different stand ages to mitigating the 'stem exclusion' process and encouraging 'understory re-initiation' process. We investigated an 82-year-old (as of 2005) sugi (*Cryptomeria japonica*) plantation with a total of six small patches of 4-, 21- and 40-year-old trees in north Kyushu, Japan. The 21-year-old patches showed the lowest species richness and individual density among the four patch/matrix ages. The 21-year-old patch adjacent to the 82-year-old matrix had more individuals and species than another 21-year-old patch. The 40-year-old patch surrounded by the 82-year matrix had a low abundance of small saplings (≥ 2 m height) of the natural forest species, which might have been recruited recently, as well as large saplings (≤ 2 m), compared with a 40-year-old patch adjacent to a 21-year-old patch and 82-year-old matrix. This result suggests that understory vegetation in the 21-year-old patches was at the stage of the 'stem exclusion' and in the 40-year-old patches was at the stage of the 'understory re-initiation' of Oliver's model. Further, we concluded that light penetration from the 82-year-old matrix mitigated 'stem exclusion' of the 21-year-old patch, and that 'understory re-initiation' was promoted by the edge effects from the 82-year-old matrix, which might have provided a better light regime than the patch interior, resulting in recruitment of more seedlings around the edge.

Keywords Patch mosaic · Stem exclusion · Vertical stratification · Light environment · Seed dispersal

Introduction

The importance of biodiversity conservation has become recognized globally, not only in native habitats, but also in modified ones, such as plantation forests, especially in regard to sustainable forest management (Nagaike 2002; Brockerhoff et al. 2017). The main issue in plantation forests in relation to biodiversity is the alteration of natural habitats with high structural complexity to even-aged monocultures with overly simplified structures (Nagaike 2000; Brockerhoff et al. 2008). However, a certain level of biodiversity can be maintained in even-aged monoculture stands during the process of stand development with appropriate management (Lindenmayer and Hobbs 2004; Ito et al. 2003). Recently, appropriate management of plantation forests for biodiversity conservation has become a requirement under OECMs (other effective area-based conservation measures) as part of the globally growing momentum of 'nature positive' (Kadoya 2022; Shiono et al. 2021).

To appropriately manage plantation forests, we should understand precisely how and when their biodiversity declines and recovers in the process of stand establishment and development. As Fujimori (2001) suggested, based on his intensive review of previous studies, it can be expected that the dynamics of natural tree populations in even-aged plantations would follow the natural model of stand development after disturbance suggested by Oliver (1981), which included four stages, i.e., 'stand initiation' in which

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new stems of plant species reoccupy the disturbed open space, 'stem exclusion' in which canopy closure results in intense competition between existing stems and limits the establishment of new stems, 'understory re-initiation' in which new stems begin to grow beneath the canopy with gap formation, and 'old growth' in which trees of various ages and sizes form the forest stand.

If so, avoidance of stem exclusion and promotion of understory re-initiation will be key to the management of plantations for biodiversity. However, it has not been fully investigated whether tree populations in even-aged plantations maintained by weeding or thinning practices follow Oliver's model of natural forests. To determine this, it is necessary to verify the changes in understory tree populations alongside the stand age of plantations from this perspective.

In addition to the decline of biodiversity at stand level, extensive even-aged plantations have strong effects on biodiversity at landscape level. Yamagawa et al. (2010) pointed out that the lack of sufficient seed sources for native trees in extensive conifer monoculture often makes it difficult to re-convert conifer plantations to semi-natural broadleaf forests. Previously, we investigated the plant species diversity of conifer plantations under a strip-clearcutting system, and observed more plant species with gravity- and frugivore-dispersed seeds in a sugi (*Cryptomeria japonica* D. Don) plantation in a strip-clear-cut site compared to a stand of the same age established after large-scale clearcutting (Ito et al. 2006a). This result indicated the possibility that some natural forest trees can be maintained as a meta-population in a strip-clearcutting system through the functioning of understory trees in the retained strip as a seed source. In this context, small-scale clearcutting, which has been attracting the attention of the Japanese government and forest managers (Forestry Agency 2022), may be an option for maintaining understory biodiversity by creating mosaics of uneven-aged plantation patches. Small-scale clearcutting can improve the light environment of the understory of adjacent closed stands through physical edge effects (Murcia 1995; Yamagawa et al. 2009). Formation of the forest edge may also encourage the maintenance and recolonization of native trees in the understory by seed dispersal from the adjacent stands (Seiwa et al. 2012; Yamagawa et al. 2013). On the basis of these studies, we can expect that these positive edge effects can mitigate 'stem exclusion' under thick conifer canopy, and promote 'understory re-initiation' from the adjacent old patches.

There are many studies on small-scale clearcutting regarding the growth of planted trees (Coates 2000; Kohama et al. 2006; Yamashita et al. 2006; Ito et al. 2006b), but there is limited information on biodiversity conservation within same-age forests with small-scale clearcutting. Yamagawa et al. (2009) studied the understory vegetation in a conifer plantation established by small-scale clearcutting and reported a clear relationship between forest age and understory plant life form composition, but did not analyze stem exclusion or understory re-invasion, in relation to the edge effects.

This study aimed to (1) verify whether the broadleaf tree populations in the understory of an uneven-aged conifer plantation followed Oliver's model of natural forest recovery, and (2) examine the contribution of forest edges between patches of different-aged stands to mitigating the 'stem exclusion' process and encouraging the 'understory re-initiation' process, by re-analyzing the data of an uneven-aged conifer plantation in Kyushu, Japan reported by Yamagawa et al. (2009) at species level.

Materials and methods

Study site

This study was conducted in a conifer plantation located in Oita Prefecture, southern Japan (33°122′N, 131°172′) (Fig. 1). The study site was situated on a gentle mountain slope 790 m above sea level. The mean annual temperature and annual precipitation over the 4-year period were approximately 13.3 °C and 2,237.5 mm, respectively. The study site has been managed by a private company (Kyusyu Rinsan Co., Inc.) as an uneven-aged forest, where sugi was planted in 1923, and then small patches of approximately 0.1 ha were established in 1965, 1984, and 2001 followed by

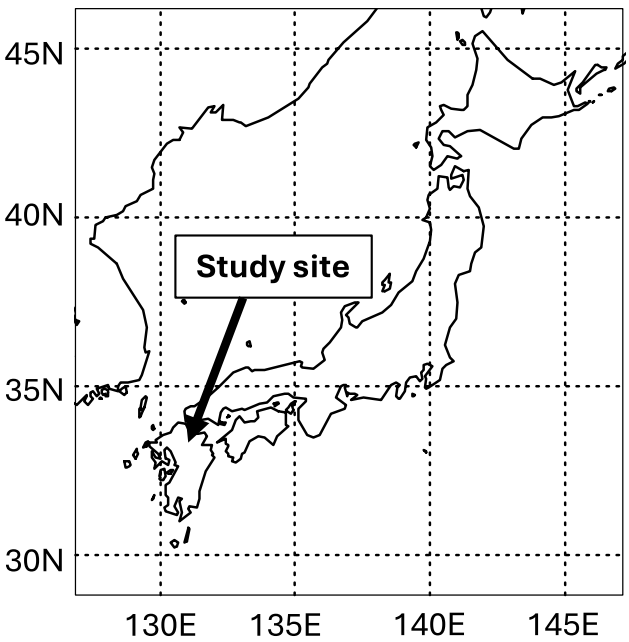


Fig. 1 Location of the study site

planting of sugi or hinoki (*Chamaecyparis obtusa* (Siebold & Zucc.) Endl.).

Field survey

A 1.4 ha study plot was established within the above stand in 2004, consisting of three, two, and one small patches established in 1965, 1984, and 2001, respectively (hereafter, 4-, 21-, and 40-year-old patches based on the middle year of the study period (2005, see below)), within a sugi stand planted in 1923 (hereafter, 82-year-old matrix) (Fig. 2a). The plot was divided into a total of 560 grids of 5 m × 5 m. All vascular plants occurring in each grid were recorded together with the species name and tree height (for individuals ≥ 0.5 m height) of understory vegetation (other than that of planted sugi or hinoki).The measurements were conducted from 2004 to 2007 for the matrix, from 2004 to 2005 for the 40- and 21-year-old patches, and in 2006 for the 4-year-old patch, respectively.

Data analysis

Plot classification

Each grid was classified into 82-year-old matrix, 40-, 21-, and 4-year-old patches according to which of the four stand ages comprised the largest proportion of the grid area. The 40- and 21-year-old patches were named 40-W, 40-S, 40-E, 21-S, 21-E, and 4-E according to their location in the plot (Fig. 2a). The 40-W patch was surrounded on all sides by 82-year-old matrix; 40-S and 21-S were adjacent to each other and surrounded by 82-year-old matrix; and 21-E and 40-E, and 40-E and 4-E were adjacent to each other and surrounded by 82-year-old matrix. The stand attributes of each patch are shown in Table 1.

Classification of tree species groups

Oliver (1981) suggested that the distribution of trees at each developmental stage differs depending on

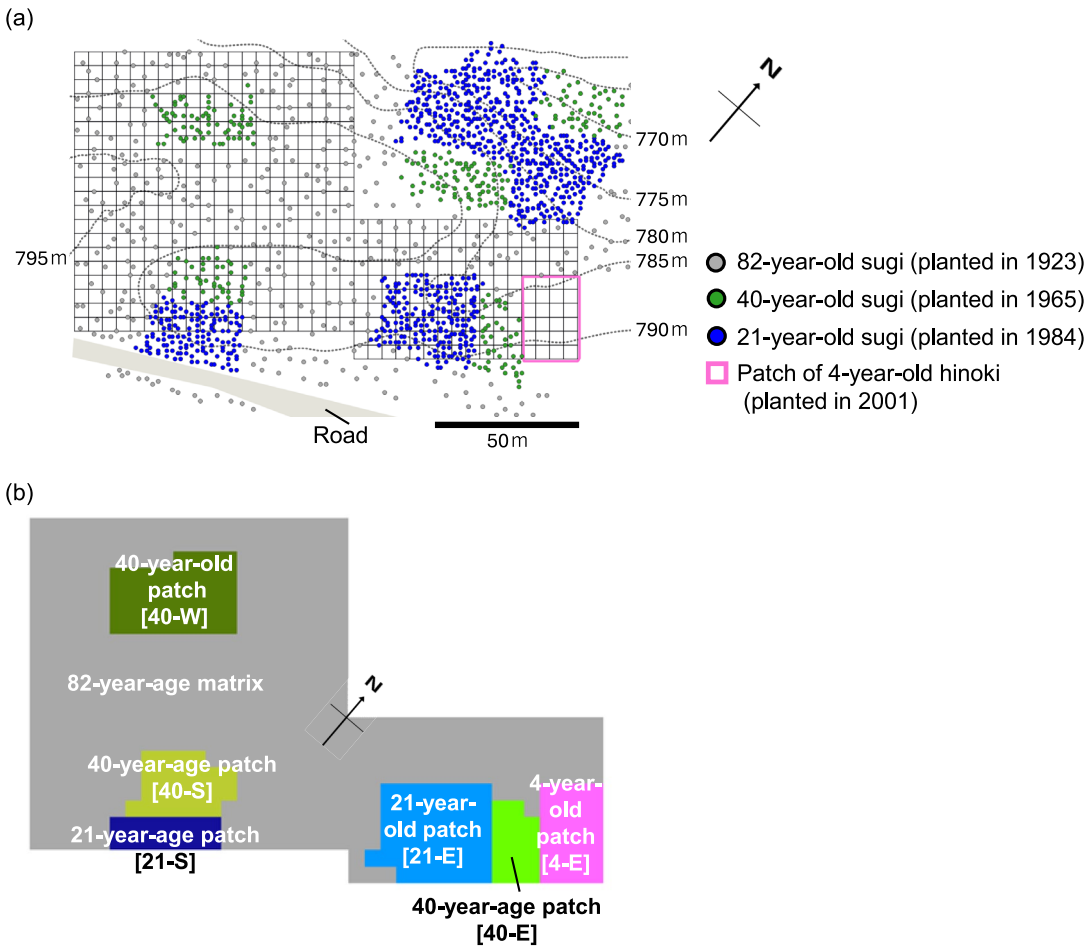


Fig. 2 Distribution of canopy trees (**a**), and patch configuration in the present study (**b**). The age of trees and patches were based on the middle year of the study period (2005)

Table 1 Summary of the attributes of the studied stand

	Planted species	Tree age	Area (ha)	Number of grids	Density (/ha)	Average tree height (m)	Average DBH (cm)
82-year-old matrix	*Cryptomeria japonica*	82	1.00	408	268	25.4	50.8
40-year-old patch	*Cryptomeria japonica*	40	0.18	72	1094	18.7	25.4
40-E			0.04	14	940		
40-S			0.05	22	1140		
40-W			0.09	36	1156		
21-year-old patch	*Cryptomeria japonica*	21	0.16	56	1664	12.3	14.6
21-E			0.12	42	1715		
21-S			0.04	14	1589		
4-year-old patch (4-E)	*Chamaecyparis obtusa*	4	0.06	24	1880	3.2	2.9
Total			1.40	560			

characteristics of the original habitats and life forms of each species. We classified the species into three groups, i.e., pioneer, coppice woodland species, and natural forest species groups, based on characteristic habitats (cf., Yamagawa et al. 2009). The major species in the study were as follows: *Rubus palmatus* Thunb and *Clerodendrum trichotomum* Thunb as pioneers, *Helwingia japonica* F. Dietr, and *Lindera sericea* Blume as the coppice woodland species which are likely to occur in frequently disturbed forest such as coppice woodlands but not have the characteristics of typical pioneer species, and *Fagus crenata* Blume and *Quercus crispula* Blume as the natural forest species which are the late-seral species of the region.

Data analysis

Height class frequency distribution was compared between patches (and the matrix) of different ages, or among patches of the same age with different positions by Kolmogorov–Smirnov test using R (ver.4.3.1; R Core Team 2023). Species–area curves of each species group were also compared between patches and the matrix. Species–area curves of each species were drawn using PC-ORD 7 (MJM Software Design, OR, USA), a personal computer-based software for vegetation analysis. By pooling two or three patches for the same age (21-year-old and 40-year-old patches), we counted the number of species specific to each stand age (those occurring in only one stand age) and species common to different stand ages, and then compared them with reference to all and each species group. To examine the spatial distribution of trees, the number of individuals in each grid was calculated and drawn by color with reference to all and each species group.

Results

Height class distribution

The pattern of height class distribution of understory broadleaf trees differed among all patches of different ages (Kolmogorov–Smirnov test: $p < 0.05$) (Fig. 3). In the 4-year-old patch, most individuals were less than 0–3 m in height, with high stem density ranging from 10,000 to 14,000/ha for trees 0–2 m in height (Fig. 3a). Most individuals (99.3% of all trees) in the 21-year-old patches also ranged in height from 0–3 m (Fig. 3b). The 40-year-old patch showed an L-shaped distribution with a greater tree height range of up to 14 m (Fig. 3c). In the 82-year-old matrix, the L-shaped distribution was clearer, and included trees of up to 18 m in height (Fig. 3d).

The 21-year-old patches had different height distribution patterns to each other (Kolmogorov–Smirnov test: $p < 0.05$). A larger number of individuals were observed in the height range of 0–2 m in 21-E (Fig. 4b) compared with 21-S (Fig. 4a), with 2,695 individuals/ha in the height range of 0–1 m in 21-E.

For the 40-year-old patches, the number of individuals in the lowest class (0.5–1 m) was far greater in 40-E (7,600/ha) than 40-S and 40-W (less than 2,000) (Fig. 5). However, the tree height distribution pattern did not differ between 40-E and 40-S (Kolmogorov–Smirnov test: $p > 0.05$) because these two patches had similar frequency distribution patterns with low relative frequency at upper classes (> 2 m in height). In contrast, the height distribution pattern of 40-W significantly differed from those of 40-S and 40-E (Kolmogorov–Smirnov test: $p < 0.05$), reflecting the higher relative frequency at the classes from 1 to 5 m in 40-W.

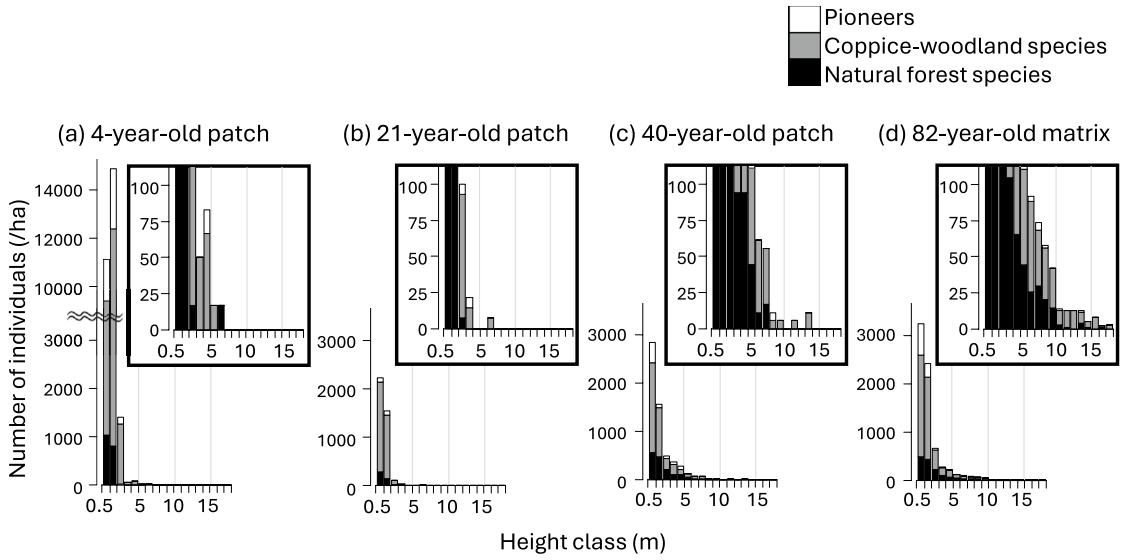


Fig. 3 Height class distribution of understory broadleaf trees in the different-age patches. Data for patches of the same age were pooled. The boxes in the upper right show a vertical expansion of the figure in the lower left

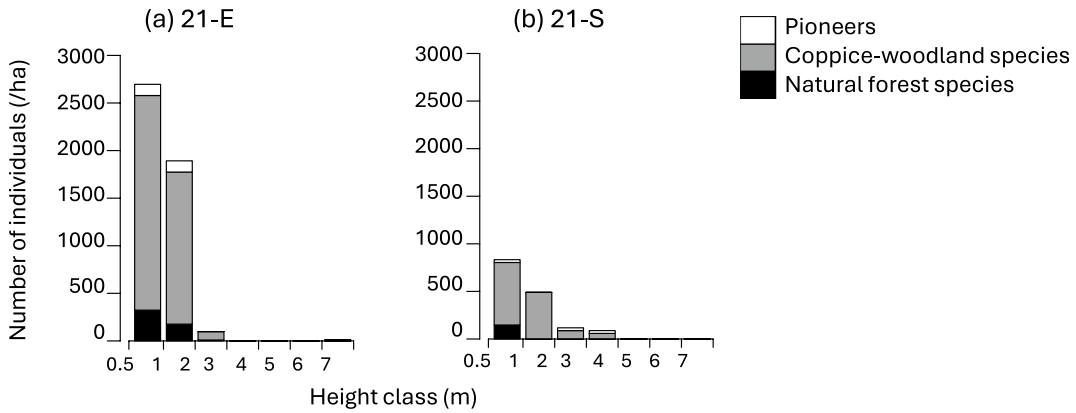


Fig. 4 Height class distribution of understory broadleaf trees in each of the 21-year-old patches

Number of species

Figure 6 shows the species–area curves drawn for all species and species group (pioneer, coppice woodland and natural forest) for patches of different ages. The 82-year-old matrix showed the overall highest species richness among the different-age patches for all species and each species group. For all species, 21-year-old patches had lower species richness compared with the patches of other ages. The 4-year-old patch had a higher pioneer and coppice woodland species richness equivalent to those in the 82-year-old matrix, but a relatively low natural forest species richness, similar to the 21-year-old patch. The 40-year-old patches showed intermediate richness among the different-age patches.

Figure 7 shows comparisons of the species–area curves among the 21-year-old patches. The species richness of 21-E was significantly higher than in 21-S, especially for coppice woodland and natural forest species. The comparisons among 40-year-old patches (Fig. 8) indicated higher species richness for every species group except for pioneers in 40-W and 40-E than in 40-S (Fig. 8a). The pioneer species richness was similar for each patch within the 40-year-old group (Fig. 8b). The coppice woodland species showed the highest richness in 40-E, followed by 40-W and 40-S, while richness of the natural forest species was highest in 40-W, followed by 40-E and 40-S.

Similarity of species occurrence among same-age patches

The 21-S and 21-E patches had 11 species in common, with 1 and 29 species specific to each patch, respectively (Fig. 9).

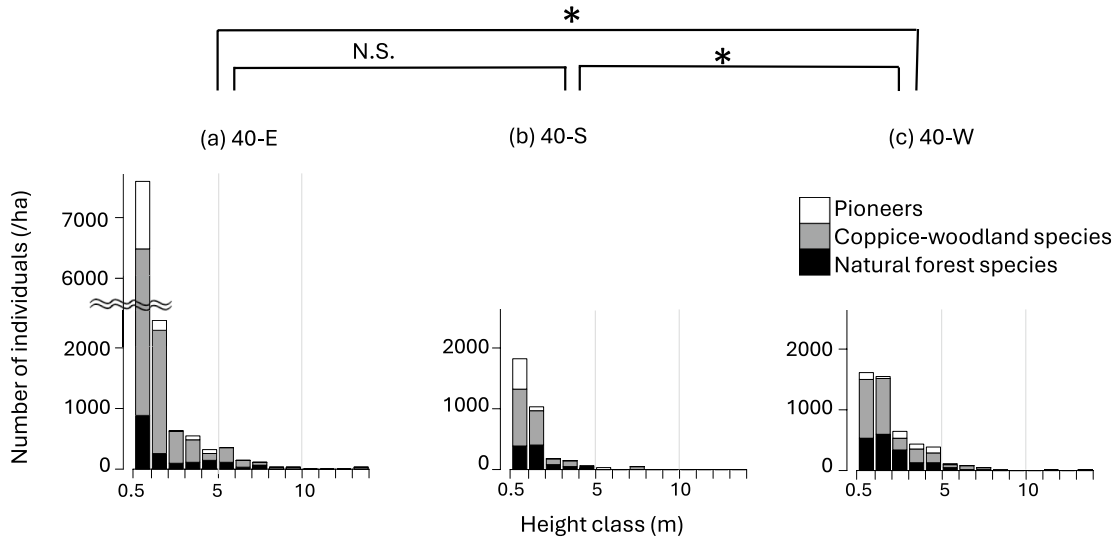


Fig. 5 Height class distribution of understory broadleaf trees in each of the 40-year-old patches. *: $p < 0.05$, N.S: $p > 0.05$ (Kolmogorov–Smirnov test)

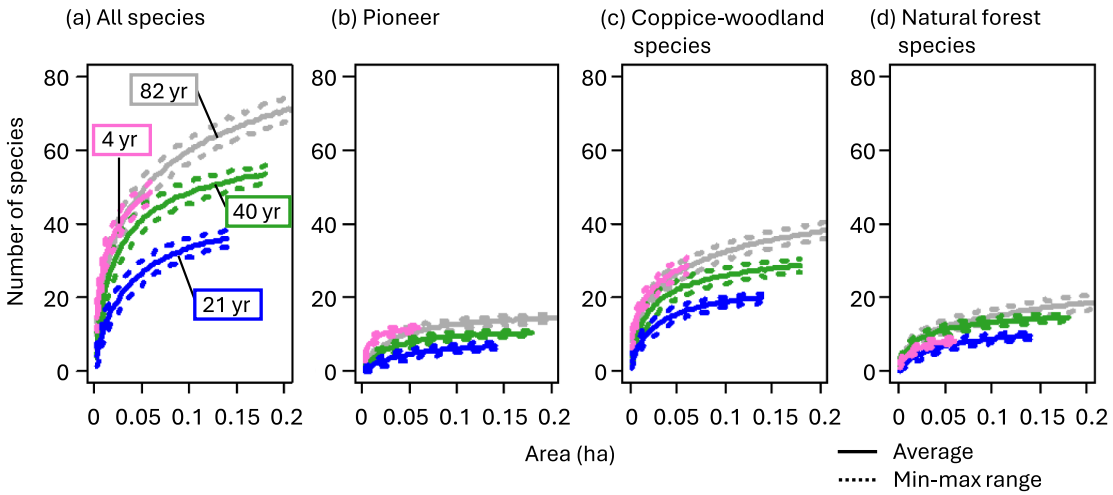


Fig. 6 Species–area curves of all species (**a**), pioneers (**b**), coppice woodland species (**c**), and natural forest species (**d**) drawn for the different-age patches. Data for patches of the same age were pooled

The species specific to 21-S was a coppice woodland species, and the 29 species specific to 21-E included 5 pioneer species, 15 coppice woodland species, and 9 natural forest species. Of the 40-year-old patches, 40-W, 40-S and 40-E had 12, 2, and 6 species specific to each patch, including 5, 1, and 0 natural forest species, respectively. The six species specific to 40-E were all coppice woodland species.

Spatial distribution

The pioneer species were distributed aggregately in the 4-year-old patch and the surrounding area in 82-year-old matrix and 40-E (Fig. 11a). The coppice woodland species also showed aggregated distribution in and around the 4-year-old patch, but were widely distributed over all the patches and the matrix (Fig. 11b). In contrast, the natural forest species were poorly represented in 40-S, 21-S and the interior of 21-E, while 40-W and the 82-year-old matrix around 40-W, the north-western part of the plot close to the adjacent broadleaf stand, showed a high density of natural forest species.

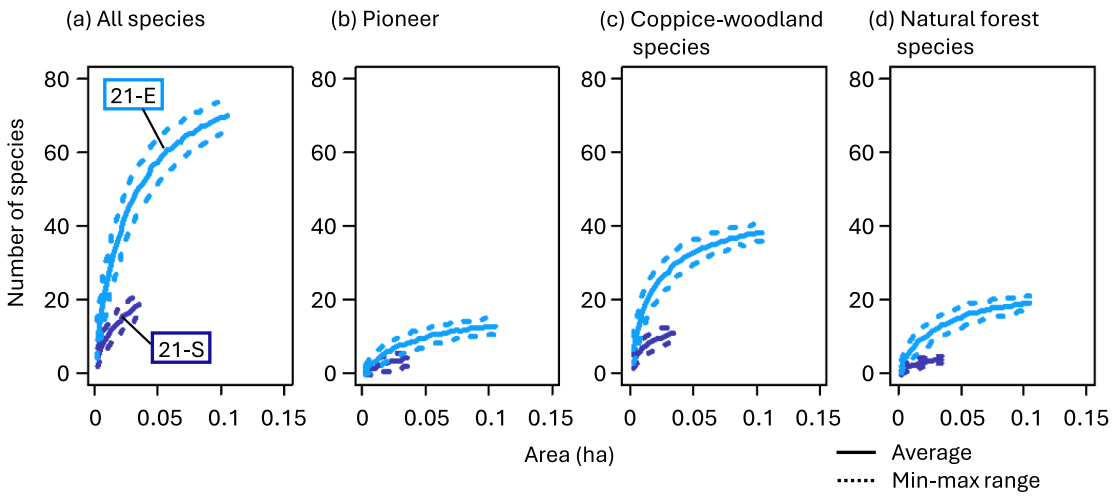


Fig. 7 Species–area curves of all species (**a**), pioneers (**b**), coppice woodland species (**c**), and natural forest species (**d**) drawn for each of the 21-year-old patches

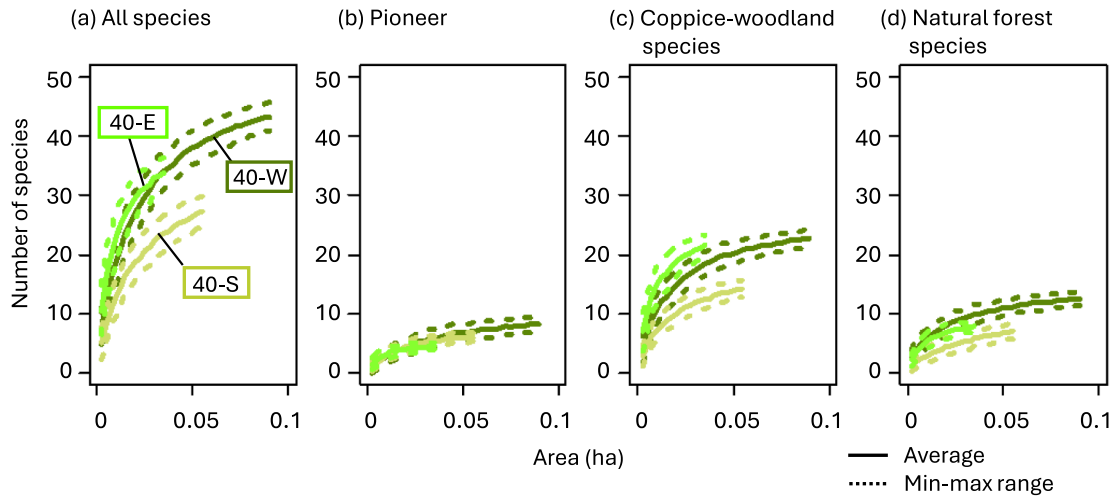


Fig. 8 Species–area curves of all species (**a**), pioneers (**b**), coppice woodland species (**c**), and natural forest species (**d**) drawn for each of the 40-year-old patches

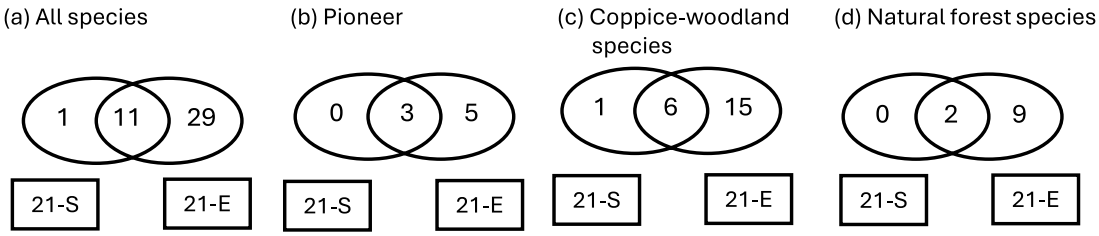


Fig. 9 Number of all species (**a**), pioneers (**b**), coppice woodland species (**c**), and natural forest species (**d**) found in each of the 21-year-old patches

Discussion

Development process of understory vegetation along the stand age

The structure of the broadleaf tree population in the understory of the studied stand varied with patch age. The 21-year-old patches showed the lowest species richness (Fig. 6), and the lowest tree density with the undeveloped height class distribution, which was concentrated in the lowest class (i.e., under 3 m, Fig. 3), among the four patch/matrix ages. This result suggests that understory vegetation in the 21-year-old patches was at the stage of the 'stem exclusion' of Oliver's stand development model (Oliver 1981). The 'stem exclusion' is a stage in which individuals with low shade tolerance die and seedlings struggle to emerge because of the limited light after canopy closure. We attributed the poor understory of the 21-year-old patches to the reduced number of individuals and species, especially of pioneer and coppice woodland species, probably due to the low light availability under the dense sugi canopy.

In contrast, the 40-year-old patches had a greater height class range with more individuals and species than the 21-year-old patches, suggesting that the understory of the 40-year-old patches was at the stage of the 'understory re-initiation'. According to Oliver (1981), the 'understory re-initiation', that is, recolonization of understory trees occurs under improved light conditions, which is dependent on the frequencies of small disturbances. In natural forests, the 'understory re-initiation' begins approximately 50 years after disturbance (Oliver 1981). For evergreen secondary forests in western Japan, Ito et al. (2009) reported that 'understory re-initiation' begins ca. 60 years after logging disturbance. However, the plantation in the present study had undergone thinning practices 25–30 years after establishment, as part of the typical management schedule of the region. This disturbance, which forms small canopy gaps, is thought to promote earlier 'understory re-initiation' (i.e., before 40 years of age), in contrast to the process in natural forests.

Previous studies have reported that the number of coppice woodland species increases in even-aged plantations after thinning (Seiwa et al. 2012; Iwakiri et al. 2019). Our results demonstrated similar trends: coppice woodland species were the most numerous among the species groups, and the older patches/matrix (40- and 82-year-old) had a greater number of coppice woodland species than 21-year-old patches. On the basis of these results combined with the previous studies, we suggest that understory development in the conifer plantation basically follows Oliver's model, and that the major recolonizing species were not natural forest species, but limited mostly to coppice woodland species.

Edge effects between different-age patches

In this study, we found that the height class distribution, number of species, and species commonality of understory vegetation differed among patches of the same age. Our results suggest that the edge effects promoted by patch arrangement have diverse effects on the development of understory vegetation. For example, between the two 21-year-old patches (21-E and 21-S) at the 'stem exclusion' stage, 21-E had more individuals (Fig. 4) and species (Fig. 7) for all species groups, and a greater number of species specific to 21-E (Fig. 9). These results indicate the possibility that the understory vegetation in 21-E was not severely suppressed compared with 21-S, even at the 'stem exclusion' stage. The patch 21-E was adjacent to the 82-year-old matrix over a wider area (i.e., a longer perimeter) than 21-S, which might have provided better light conditions via a relatively sparse canopy consisting of large trees. Thus, we concluded that light penetration (the physical edge

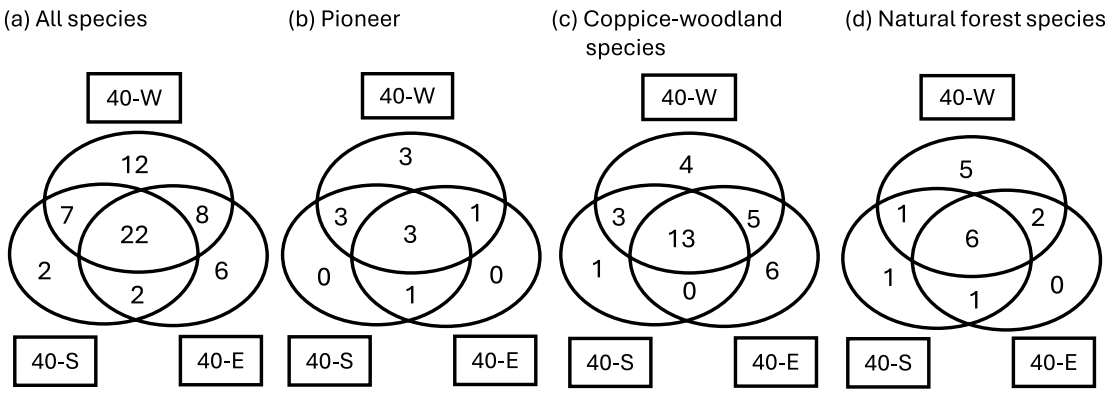


Fig. 10 Number of all species (**a**), pioneers (**b**), coppice woodland species (**c**), and natural forest species (**d**) found in each of the 40-year-old patches

effect) from the 82-year-old matrix mitigated stem exclusion in 21-E. In fact, the spatial distribution of understory individuals showed more pioneer and natural forest trees around the edge facing the 82-year-matrix (Fig. 11). In contrast, 21-S, which faced one of the 40-year-old patches (40-S), included only a few pioneer and natural forest tree individuals. This might have been due to the relatively thick canopy of the 40-year-old patch, which would have limited the light conditions of adjacent 21-S.

The differing edge effects on the understory vegetation were also observed for the 40-year-old patches at the 'understory re-initiation' stage. Among the 40-year-old patches, 40-W, which was surrounded by the 82-year matrix, had a high abundance of small saplings (shorter than 2 m in height) of natural forests species, which might have been recruited recently, as well as large saplings (taller than 2 m) compared with 40-S (Fig. 5). This suggests that 'understory re-initiation' was promoted by the edge effects from the 82-year-old matrix, which might have provided a better light regime than the patch interior, resulting in recruitment of more seedlings around the edge. The understory tree distribution showed a high density of natural forest tree species in this patch similar to the 82-year-old matrix (Fig. 11d). The number of species was also highest in 40-W among the three patches of the same age (Figs. 8 and 10). This result suggests a possibility that the 82-year-old matrix, which

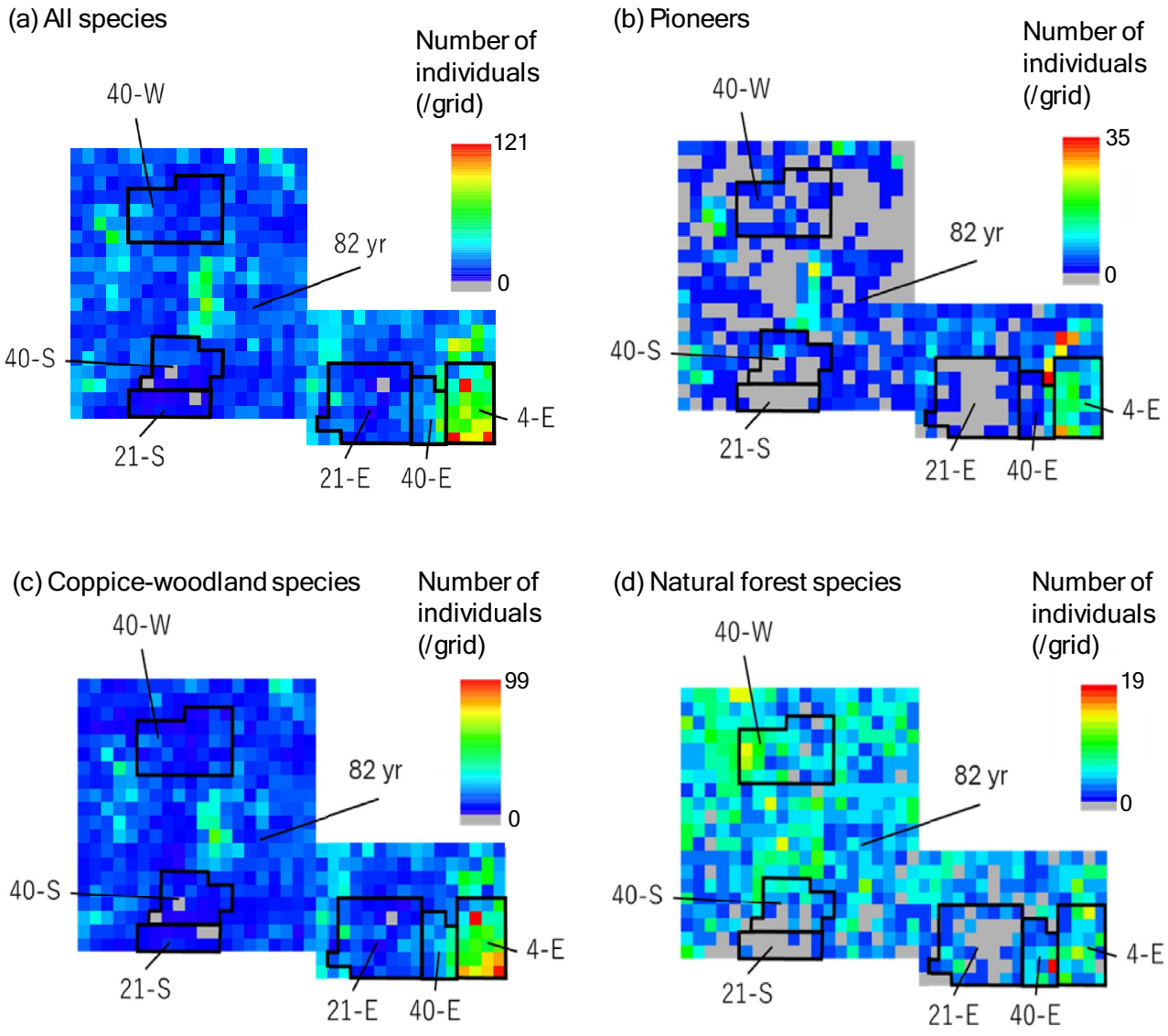


Fig. 11 Number of individuals of all species (**a**), pioneers (**b**), coppice woodland species (**c**), and natural forest species (**d**) drawn for each grid for each tree species group

included many large broadleaf trees in the understory, acted as a seed source for natural forest species and provided their seeds to 40-W as a biological edge effect combined with edge-promoted seed dispersal by birds. Ito et al. (2006a) also reported the similar edge effects under strip-clearcutting forestry. The presence of many large saplings (> 2 m in height) might have been due to mitigated 'stem exclusion' in which many individuals survived as a result of the past effects of the surrounding 82-year-old matrix, similar to 21-E.

In contrast to 40-W, 40-S, which also had a long perimeter bordering the 82-year-old matrix, did not have many trees over 2 m in height (Fig. 5). Although our data cannot clearly show the reason for this, there was a possibility that the adjacent 21-S patch, which might have had a high tree density and thick canopy of planted sugi before thinning, gave a negative edge effect by forming a darker understory around the edge within 40-S than 40-W. Apart from coppice woodland species, the tree distribution also showed a low density of understory trees around the south-facing edge adjacent to 21-S (Fig. 11).

In the case of 40-E, combined effects from several adjacent patches can be assumed. The youngest patch (4-E) with its open, short hinoki canopy could provide much better light conditions to 40-E at the edge; the recent seedling establishment and vigorous growth, that is, promoted 'understory re-initiation', was evident in the far greater number of short saplings (< 2 m in height) (Fig. 5a). The large number of individuals of natural forest species (Figs. 5a and 11d) might have resulted from the previous effects of the 82-year-old matrix before the preceding trees in 4-E were logged, similar to 40-W. We estimate that these combined effects resulted in a species-rich, large sapling-abundant understory compared with the other two patches of the same age.

However, with respect to spatial distribution, the distribution of natural forest group trees in 40-W was found to have a similar bias to the distribution of natural forest group trees in the 82-year-old matrix, so the expansion of the distribution of trees in the natural forest group may have been influenced by the concentration of trees serving as seed sources.

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Declarations

Conflict of interest We declare no conflicts of interest.

Ethical approval All experiments in the present study were compliant with the current laws of the country, Japan, in which they were performed.

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