Stand structure of a fragmented evergreen broad-leaved forest at a shrine and changes of landscape structures surrounding a suburban forest, in northern Kyushu

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Abstract: Stand structure such as species composition and canopy gap formation in a fragmented evergreen broad-leaved forest and changing patterns of a matrix surrounding the forest over the past 42 years based on vegetation maps made from aerial photos were examined. The suburban landscape had changed significantly. Some forest-type elements such as scrub and secondary deciduous broad-leaved forests had decreased in area, although plantations, *Phyllostachys* forests and secondary evergreen broad-leaved forests had increased in area. The area of the fragmented forest, which was well-developed secondary evergreen broad-leaved forest at a shrine, had not significantly changed. Some species such as *Distylium racemosum*, *Persea thunbergii*, *Camellia japonica* and *Eurya japonica* regenerated in the forest the same way as in old-growth evergreen broad-leaved forests, suggesting that population structure and dynamics of those species were not greatly influenced by landscape ecological factors or secondary succession of the forest. Regeneration behaviour of some species such as *Neolitsea sericea* and *Quercus salicina* in the forest differed significantly from that in the old-growth forests. Furthermore, the density of *N. sericea* seedlings was extremely high, although only a few mature individuals and saplings of the species occurred in the forest. Population structure of the species might be influenced by changing patterns of the matrix surrounding the fragmented forest.

Key words: canopy gaps, evergreen broad-leaved forest, matrix, seedling bank, secondary succession

真鍋 徹・鹿嶋秀子・伊東啓太郎：都市近郊域における孤立社叢林の林分構造と周辺地域の景観構造の変遷

摘要：北部九州の都市近郊域における景観構造の変遷を解析するため、1947年及び1989年撮影の空中写真から両年の植生図を作成した。あわせて、当該地域に残存する常緑広葉樹が優占する孤立した社叢林の林分構造を調査した。過去42年間に当該地域では、低木林や落葉広葉樹二次林などの面積が減少し、竹林や常緑広葉樹二次林の面積が増加した。林分構造を調査した常緑広葉樹社叢林は、過去から既に孤立状態にあり、その面積はほとんど変化していなかった。イスノキ、タブノキ、ヤブツバキ、ヒサカキなどの樹種は、当社叢林においても常緑広葉樹天然林と同様の更新状況にあると判断された。一方、シロダモやウラジロガシは、天然林とは異なった更新状況を示し、当社叢林を取り巻く景観構造の変化の影響を受けている可能性が示唆された。特に、シロダモは種子供給源となり得る成木個体数に比して非常に多量の実生が存在していた。これは、面積が増加した常緑広葉樹二次林から当該林への種子散布量の増加に起因するものと推測された。

キーワード：林冠ギャップ、常緑広葉樹林、マトリックス、実生バンク、二次遷移

1. Introduction

Most forests located in suburbs in Japan have been fragmented into small stands in recent decades (Hattori et al., 1994; Iida & Nakashizuka, 1995; Fukamachi et al., 1996). Stand structure of those isolated fragments is influenced not only by the landscape ecological characteristics of the fragments, such as their shape and size, but by those of the area surrounding the fragments (the matrix), such as connectivity and changing patterns of the elements within the matrix (Forman, 1995).

Most suburban forests had been maintained as copice for producing firewood, charcoal and fertilizer for centuries in Japan, although the forests have been abandoned since the late 1960s when fossil fuels, electricity and artificial fertilizer came into wide use (e.g. Kamada & Nakagoshi, 1990, 1997; Hong et al., 1995). The structure of plant communities in those abandoned secondary forests changed, because of the progression of secondary succession (Kamada & Nakagoshi, 1990). Furthermore, the role of canopy gap dynamics mediated by natural disturbances becomes more important for community dynamics, even in sec-

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ondary forests, as secondary succession reaches the later stages (Clebsch & Busing, 1989; Yamamoto & Manabe, 1997).

Stand characteristics such as community structure and dynamics in suburban secondary forests are, therefore, influenced not only by the landscape ecological factors such as fragmentation and characteristics of the matrix, but also by the synecological factors such as secondary succession and gap dynamics.

For young secondary forests, it might be hard to clarify that what kinds of factors significantly affect the structure or dynamics of the forest communities. Therefore, we chose a developed secondary evergreen broad-leaved forest isolated from a surrounding matrix as our study stand to diminish the effects of secondary succession on the structure and dynamics of the forest community. In this paper, we address stand structure of the isolated forests and structure and dynamics of a matrix surrounding the forest in a suburb. We also discuss the relations between landscape ecological characteristics of the area and the stand structure of the forest.

2. Study Site

The study stand was established in a secondary evergreen broad-leaved forest at the Hakusan-Taga Shrine (lat. 33°45'N, long. 130°55'E, 280 m a.s.l.) located in a suburb of Kanda-machi, northern Fukuoka (Fig. 1). Several past documents regarding the shrine show that it met the devastation of wars and was burnt sometime in the middle to the late 1600s (Nagamine & Ueda, 1996). That is, the forest had often been disturbed by strong and frequent anthropogenic factors in the past. The forest, however, has been free from severe human disturbance for hundreds of years, because it has been regarded as sacred by an ancient religion. Thus, the forest might be at the late stages of

secondary succession (Manabe et al., 2000a).

3. Methods

3.1 Landscape structure

The suburban landscape in the 2 km×2 km area on which the forest at the shrine (shrine forest) was approximately centred was clarified using actual vegetation maps in two different years. The vegetation maps at a scale of 1:10,000 were made using aerial photographs taken in 1947 and 1989. The maps were scanned using an Epson es-8000 image scanner and were digitized. The area of each landscape element was calculated as the number of pixels constituting the element. The software Photoshop version 5.0 (Adobe System Inc.) was used for calculation of the pixels.

3.2 Stand structure

A 50 m×50 m plot (P1) and two 30 m×30 m plots (P2 and P3) were established at the shrine forest in November 1994 and May 1995 (Fig. 2). We classified each individual tree into one of three size-based classes: mature individuals, which were larger than 5 cm diameter at breast height (dbh); saplings, which were larger than 1.3 m in height and smaller than 5 cm dbh; and seedlings, which were larger than 0.1 m and smaller than 1.3 m in height. All mature individuals were identified by their species names and their dbh was measured.

Ten 10 m×10 m quadrats were set in P1, and each of five 10 m×10 m quadrats were set in P2 and P3. The quadrats with a canopy cover of <30% were considered to be gap quadrats. Of 20 quadrats, 17 were beneath a closed canopy and three were in the canopy gaps. The species names of all saplings in the quadrats were recorded. All mature trees and saplings had their vertical position recorded: canopy individuals that reached the forest canopy, and understorey individu-

Fig. 1 Location of the study site.

図-1 調査地の位置

Fig. 2 Research design of the plots.

図-2 設置したプロットの概要

als that did not reach the forest canopy.

Sub-quadrats, 5 m×5 m, were positioned in all 20 quadrats. Six 1 m×1 m sub-quadrats were also positioned in the canopy gaps in P1. For all seedlings in the sub-quadrats, species names and heights were recorded, except for shrub species and lianas, which could not be individually identified owing to their creeping form. Data sets obtained in each plot were integrated for analysis.

For all canopy gaps formed in the forest, the largest distance between the gap edges (length), the largest distance perpendicular to length (width), species identity, and the type of injury or cause of death of gap makers were recorded.

Nomenclature follows that of Ohwi & Kitagawa (1983).

4. Results

4.1 Landscape structure

The suburban landscape analyzed consisted of 12 and 13 types of landscape elements in 1947 and 1989,

respectively (Figs. 3 & 4, Table 1). The shrine forest could clearly be distinguished from other forest type elements within the landscape as a developed secondary evergreen broad-leaved forest, because tall evergreen broad-leaved trees having large crown in both years dominated the canopy layer of the forest. Other forest-type elements were also distinguishable: secondary evergreen broad-leaved forest (evergreen forest), which was composed of many evergreen broad-leaved trees with small crowns; secondary evergreen and deciduous broad-leaved mixed forest (mixed forest), which was characterized by a canopy dominated by both evergreen broad-leaved trees and deciduous broad-leaved tree; secondary deciduous broad-leaved forest (deciduous forest), which was mainly composed of deciduous broad-leaved trees with small crowns; scrub, which had various components, almost all of which were small trees or shrubs with very small crowns; and plantation, which was a mono-culture of evergreen needle-leaved trees such as *Cryptomeria japonica* (Linn. fil.) D. Don and *Chamaecyparis*

Fig. 3 Vegetation map at the study site in 1947.

図-3 調査対象域の相観植生図 (1947 年)

Fig. 4 Vegetation map at the study site in 1989.

図-4 調査対象域の相観植生図 (1989 年)

obtusa (Sieb. et Zucc.) Sieb. et Zucc., apud Endl.

Agricultural fields (paddy fields and crop lands) were the most common land cover (34.0% of total area), followed by scrub (26.1%), secondary grasslands (13.3%) and deciduous forests (11.4%) in 1947. Plantations had become the most dominant elements (27.4%), followed by agricultural fields (20.4%), secondary grasslands (8.9%) and *Phyllostachys* forests (8.4%) in 1989. Artificial lawn and meadow, and *Cryptomeria japonica* and *Phyllostachys* spp. mixed forests, which did not exist in 1947, also occurred in 1989.

Over the past 42 years, some elements such as scrub, agricultural fields, secondary grasslands and deciduous forests have significantly diminished in area, although other elements such as plantations, evergreen forests and *Phyllostachys* forests increased their area.

The shrine forest did not significantly change in area, although a small part of it changed into plantation (Fig. 5). Most of the scrub and deciduous forests

in 1947 changed to plantations, although some did change to evergreen forests and mixed forests. On the other hand, most of evergreen forests in 1989 were derived from other forest-type elements such as mixed forests, deciduous forests and scrub.

4.2 Stand structure

Among 15 canopy gaps formed in the shrine forest, the causes of gap formation were identified in 11 (Table 2). A single treefall formed 53.3% of all gaps, and multiple treefalls formed 20.0%. Four gaps for which the cause of gap formation was not identified were regarded as very old, because the degree of rotting in the gap-makers was high. Those old gaps were partly closed by lateral expansion of the tree branches surrounding the gaps. Most of the gap-makers were *Castanopsis cuspidata* (Thunb.) Schottky (Table 3). Among gap-makers, four individuals were thought to be resprouted ones because of their multiple stems. All gap-makers were snapped except for one individual that formed a gap by its inclination. Among snapped gap-makers, three individuals might have

Table 1 Size of landscape elements consisted of suburban landscape analyzed in 1947 and 1989**表-1** 1947年および1989年における調査対象域の景観構成要素の面積

Landscape element	1947		1989	
	Size (ha)	Ratio (%)	Size (ha)	Ratio (%)
Developed secondary evergreen broad-leaved forest	4.2	1.1	3.8	0.9
Secondary evergreen broad-leaved forest	1.2	0.3	20.4	5.1
Secondary evergreen and deciduous broad-leaved mixed forest	17.8	4.4	11.7	2.9
Secondary deciduous broad-leaved forest	45.5	11.4	28.9	7.2
Scrub	104.5	26.1	—	—
Secondary pine forest	4.5	1.1	4.9	1.2
Plantation (<i>Cryptomeria japonica</i> and <i>Chamaecyparis obtusa</i>)	2.5	0.6	109.4	27.4
<i>Phyllostachys</i> forest	6.4	1.6	33.7	8.4
<i>Cryptomeria</i> and <i>Phyllostachys</i> mixed forest	—	—	14.4	3.6
Secondary grassland	53.3	13.3	35.6	8.9
Cut-over land	3.3	0.8	0.5	0.1
Artificial lawn and meadow	—	—	2.5	0.6
Agricultural field	135.9	34.0	81.7	20.4
Others	20.9	5.2	52.5	13.3
Total	400.0	100.0	400.0	100.0

Table 2 Type of injury of gap-makers in the shrine forest**表-2** 社叢林における林冠ギャップ形成木の死傷形態

Number of gap-makers creating a gap	Type of injury		
	Snapped	Snapped + incline	Unknown
Single stem	8	0	—
Multiple stems	2	1	—
Unknown	—	—	4

Table 3 Species and the number of gap-makers creating canopy gaps in the shrine forest**表-3** 社叢林における林冠ギャップ形成木の種別幹数

Species and stem form of gap-makers	Number of gap-makers
<i>Castanopsis cuspidata</i>	
Single stem	8
Multiple stems	4
<i>Symplocos lucida</i>	
Single stem	2
<i>Prunus jamasakura</i>	
Multiple stems	1

broken their stems after they died. We could not clarify the ultimate causes of death of those stems (e.g., strong typhoon winds, competition amongst stems, a natural death), although eight gap-makers were thought to have been snapped by strong winds. The average gap size was 54.7 m² and ranged from 7.8 m² to 203.6 m².

Among 57 woody species that were identified in the shrine forest, 56% of them were evergreen broad-leaved species (Appendix 1). Mature individuals were composed of 39 species, and their density and total basal area of their stems were 937 ha⁻¹ and 51.96 m² ha⁻¹, respectively. *Symplocos lucida* Sieb. et Zucc. was the most numerous, followed by *Castanopsis cuspidata*, *Persea thunbergii* (Sieb. et Zucc.) Kosterm., *Camellia japonica* Linn. and *Distylium racemosum* Sieb. et Zucc. (Table 4). Basal area of each species was also larger in evergreen broad-leaved trees such as *C. cuspidata*, *D. racemosum*, *P. thunbergii*. The deciduous tree *Cornus brachypoda* C. A. Mey. was fourth largest in basal area. The forest canopy was also dominated by evergreen broad-leaved trees such as *Castanopsis cuspidata*, *Distylium racemosum* and *Persea thunbergii*.

Saplings were composed of 32 species, including shrubs such as *Callicarpa mollis* Sieb. et Zucc., *Aucuba japonica* Thunb. and *Maesa japonica* (Thunb.) Moritzi. The number of individuals was largest for *A. japonica*, and sub-canopy trees such as *Symplocos lucida*, *Ilex rotunda* Thunb., *Camellia japonica* and *Eurya japonica* Thunb. were also abundant. *Cornus brachypoda* and *Rhus succedanea* Linn., which were abundant as mature individuals, had no saplings. Some canopy and sub-canopy trees such as *Clerodendron trichotomum* Thunb. and *Prunus spinulosa* Sieb. et Zucc. had many saplings, although there were no mature individuals of these.

Fig. 5 The change of major landscape elements over the past 42 years. Left and right lines show landscape elements in 1947 and those in 1989, respectively. Patterns of arrows indicated categorized changing rate of the size of the elements: the ratios of the size of each element in 1989, which had been a certain element in 1947, to the size of the certain element in 1947 were divided into six classes. Abbreviations: DEB, developed secondary evergreen broad-leaved forest; SEF, secondary evergreen broad-leaved forest; SMF, secondary evergreen and deciduous broad-leaved mixed forest; SDF, secondary deciduous broad-leaved forest; S, scrub; P, plantation; PF, *Phyllostachys* forest.

図-5 42年間に於ける主要な景観構成要素の変化パターン
左列および右列に、1947年および1989年における景観構成要素を示した。矢印の凡例は、各景観構成要素の面積の変化割合を示す：1947年に、ある景観構成要素であったものが、1989年に、どの景観構成要素にどの程度変化したかを6段階で示した。DEBは発達した常緑広葉樹二次林、SEFは常緑広葉樹二次林、SMFは常緑広葉樹・落葉広葉樹混交二次林、SDFは落葉広葉樹二次林、Sは低木林、Pは植林地、PFは竹林を示す。

Seedlings were present from 46 species, and their density was 19,568 ha⁻¹. All species that had mature individuals also had seedlings, except for *Acer palmatum* Thunb. and *Symplocos myrtacea* Sieb. et Zucc. Some canopy and sub-canopy trees, such as *Celtis sinensis* Pers. var. *japonica* (Planch.) Nakai, *Carpinus tschonoskii* Maxim. and *S. prunifolia* Sieb. et Zucc., as well as some shrubs, such as *Viburnum erosum* Thunb., *Zanthoxylum schinifolium* Sieb. et Zucc. and *Euonymus sieboldianus* Blume, had seedlings, although they had no mature individuals and saplings.

Abundant seedlings occurred beneath a closed canopy for *Distylium racemosum*, *Quercus salicima*

Blume and *Cleyera japonica* Thunb. pro p., emend. Sieb. et Zucc., although their seedlings did not occur in the canopy gaps (Table 4). *Castanopsis cuspidata* and *Symplocos lucida* had more seedlings beneath a closed canopy than in the canopy gaps. *Persea thunbergii*, *Neolitsea aciculata* (Blume) Koidz., *N. sericea* (Blume) Koidz., *Eurya japonica*, *Prunus spinulosa* and *Zanthoxylum ailanthoides* Sieb. et Zucc. had more seedlings in the canopy gaps than beneath a closed canopy. Only seedlings of *Camellia japonica* occurred almost equally both beneath a closed canopy and in the canopy gaps.

5. Discussion

5.1 Characteristics of the landscape and the forest

The suburban landscape of the 2 km×2 km area on which the shrine forest was approximately centred had significantly changed over the past 42 years. In 1989, scrub, which had been the most dominant element in 1947, had vanished in the landscape, and evergreen forests had become one of the predominant elements. Scrub elements in 1947 were composed of small individuals having similar height and crown width, indicating that the elements were established after clear-cutting of coppice. Thus, coppice had often used by human, and had widely distributed in the landscape in 1947.

On the other hand, evergreen forests had increased their area in 1989. The forests had mainly changed from scrub, deciduous forests, and mixed forests. This change in landscape elements was attributed to socio-economic changes in the late 1960s (Kamada & Nakagoshi, 1990). That is, the progress of secondary succession owing to these socio-economic changes was from scrub, deciduous forests and mixed forests to evergreen forests. Similar results were reported for another area in Japan (Hong et al., 1995; Kamada & Nakagoshi, 1996, 1997). Increased *Phyllostachys* forests had previously been scrub, deciduous forests, mixed forests in 1947. Expansion of *Phyllostachys* forests, which is widely reported in recent decades in Japan, might be attributable to the same socio-economic changes (Okutomi et al., 1996).

The shrine forest was set in a matrix that was composed of various different kinds of landscape elements in 1947 as well as in 1989. The total area of the forest has not changed largely. The forest, therefore, had already been an isolated fragment in 1947, and the degree of fragmentation did not change much over 42 years.

Composition of canopy trees in this fragmented shrine forest is relatively similar to that in old-growth evergreen broad-leaved forest in Aya Town, Miyazaki Prefecture (Tanouchi & Yamamoto, 1995) and Is. Tsushima, Nagasaki Prefecture (Manabe et al., 2000b), which have wide areas. However, the maximum dbh of

Table 4 The density (ha^{-1}) of canopy individuals, understory individuals and seedlings of major woody species in the shrine forest
 表-4 社叢林における主要樹種の林冠層到達個体, 下層個体および実生個体の密度 (ha^{-1})

Species	Canopy individuals	Understory individuals	Seedlings	
			Closed canopy	Canopy gaps
<i>Distylium racemosum</i>	56	121	729	0
<i>Quercus salicina</i>	5	24	518	0
<i>Cleyera japonica</i>	2	77	118	0
<i>Castanopsis cuspidata</i>	128	90	964	328
<i>Symplocos lucida</i>	12	443	1,387	820
<i>Camellia japonica</i>	2	211	2,515	2,950
<i>Persea thunbergii</i>	40	98	353	492
<i>Neolitsea sericia</i>	2	37	5,147	7,048
<i>Neolitsea aciculata</i>	2	20	282	1,967
<i>Zanthoxylum ailanthoides</i>	2	0	24	656
<i>Eurya japonica</i>	0	200	353	983
<i>Prunus spinulosa</i>	0	10	47	6,228

major dominants such as *Castanopsis cuspidata*, *Distylium racemosum* and *Persea thunbergii* were only half of those in the old-growth forests. Those findings indicate that the forest is located at the relatively late stage of secondary succession in the warm-temperate region in Japan. In addition, the species composition in the forest in 1947 may not differ much from that in 1989.

Thus, landscape ecological characteristics as well as synecological characteristics of the fragmented shrine forest have not changed significantly, although the suburban landscape surrounding the forest has changed much over the last 42 years.

5.2 Population structure of major woody species

Characteristics of seedling banks are important for clarifying their regeneration behaviour (e.g. Harper, 1977). Major species were classified into four groups based on the emergence pattern of their seedlings in the forest: species having abundant seedlings only beneath a closed canopy, those having more seedlings beneath a closed canopy than in the canopy gaps, those having more seedlings in the canopy gaps than beneath a closed canopy, and those having seedlings almost as numerous both beneath a closed canopy and in the canopy gaps.

Distylium racemosum formed substantial seedling banks only beneath a closed canopy in this forest. The species maintains its population through abundant seedlings with high survival rate based on strong shade tolerance in the old-growth evergreen broad-leaved forests (Yamamoto, 1992; Sato et al., 1994; Tanouchi et al., 1994). The species may regenerate successively in the forest as well as in the old-growth forests, although the reasons that no seedlings occurred in the canopy gaps in the forest could not be determined in this study.

The density of *Castanopsis cuspidata* seedlings was low within gaps as well as beneath a closed canopy in

the old-growth forests (Yamamoto, 1992), indicating that the species has a relatively weak shade tolerance (Tanouchi, 1990). Catastrophic natural disturbances such as occasional strong typhoons and landslides might be effective for successful regeneration of the species in the old-growth stands (Yamamoto, 1992). Abundant seedlings of the species, however, occurred in the canopy gaps in the old-growth evergreen broad-leaved forests without *D. racemosum*, suggesting that regeneration behaviour of the species varies with stand structure, especially the presence or absence of important dominant species (Yamamoto, 1994). The density of *C. cuspidata* seedlings was high, although *D. racemosum* mature individuals also occurred in the forest. The high density of *C. cuspidata* may be due to a varying micro-environmental condition in the forest following fragmentation. Nevertheless, the density of the seedlings was higher beneath a closed canopy than in canopy gaps, suggesting that the species might be able to form considerable seedling banks in forests in case the density of *D. racemosum* mature individual becomes relatively low in the forests.

More seedlings occurred in the canopy gaps than beneath a closed canopy for *Persea thunbergii* and *Eurya japonica* in the forest. The seeds of those species might disperse widely over the forest, as their seeds are often dispersed by birds (Manabe et al., 1993; Kominami et al., 1995). In the old-growth forests, seedling banks contribute largely to successive regeneration for *P. thunbergii* (Yamamoto, 1992; Sato et al., 1994; Tanouchi et al., 1994) and *E. japonica* (Manabe & Yamamoto, 1997). Shade tolerance might be lower for *P. thunbergii* than for other major canopy species such as *Distylium racemosum* and *Quercus salicina* (Sato et al., 1994). However, *P. thunbergii* and *E. japonica* might maintain their seedling banks by an abundant seed supply in the forest as seen in old-growth forests and other secondary forests (Manabe et

al., 1993; Sato et al., 1994; Manabe & Yamamoto, 1997).

Cleyera japonica and *Camellia japonica*, which are typical sub-canopy species in the old-growth forests, have high seedling densities, and maintain their population successively beneath a closed canopy in the old-growth forests (Yamamoto, 1992). These species could also regenerate successively beneath a closed canopy in the forest as well as in the old-growth forests.

Zanthoxylum ailanthoides and *Prunus spinulosa*, which are typical pioneer trees, had high seedling density in the gaps, although they had few mature individuals. Seedlings of some pioneer canopy trees established vigorously in large gaps and gaps formed by uprooted trees with exposed mineral soil (Putz, 1983; Brokaw, 1985; Nakashizuka, 1989). In the old-growth evergreen broad-leaved forest at the Aya Research Site in Miyazaki Prefecture, the density of *Z. ailanthoides* mature individuals was very low, suggesting that the species requires catastrophic disturbances for population maintenance (Yamamoto, 1992). Abiotic factors within the isolated fragments differ from those in continuous forests having large and undisturbed areas. However, some physical micro-environments such as light and soil moisture in the fragments become similar to those in large gaps in continuous forests (Murcia, 1995). Abundant seedlings of the species may be partly due to the varied micro-environmental conditions following fragmentation. However, very few saplings and mature individuals occurred in the forest, although the degree of fragmentation of the forest did not change much over 42 years. Furthermore, the species can regenerate in some gaps formed under ordinal disturbance regimes in the other evergreen broad-leaved forest at Mt. Kasugayama in Nara Prefecture (Shimoda et al., 1994). Thus, abundant seedlings of the species might just respond to canopy gap formation, since most seedlings occurred in the gaps in the forest.

The above species, therefore, might maintain their population by the same regeneration behaviour both in the forest and in the old-growth forests. This suggests that population structure and dynamics of these species might not be influenced by landscape ecological factors such as the fragmentation and the change in a matrix.

On the other hand, many seedlings of *Quercus salicina* occurred only in the gaps, as for *Distylium racemosum*. Seedlings of *Q. salicina* have less shade tolerance than *D. racemosum* (Tanouchi, 1990; Tanouchi & Yamamoto, 1995). *Q. salicina* has relatively meagre seedling banks, and needs large canopy gaps for recruiting into the upper layer (Yamamoto, 1992; Tanouchi & Yamamoto, 1995). This species, therefore, might regenerate differently in the forest than in the old-growth forests. The reasons why the species varies its regeneration behaviour could not be determined in

this study.

Neolitsea sericia had very high seedling density, although mature individuals that might be able to produce seeds were very few in the forest. This finding suggests that most *N. sericia* seedlings might come from seeds produced outside the forest and dispersed into the forest by birds, because the species produces endozoochory seeds. Evergreen broad-leaved coppices are dominant secondary forests in Kyushu, and *N. sericia* occur widely in this type of secondary forest in northern Kyushu (Miyawaki, 1981). Seed sources of the species in the forest are largely attributable to the evergreen forests and mixed forests, which increased their total area in the previous decades. Thus, population structure and dynamics of the species are affected by the changing patterns of the matrix. It is, however, unclear whether population dynamics of other evergreen trees producing endozoochory seeds are influenced significantly by landscape ecological factors.

Thus, we should pay attention to the landscape ecological factors, as well as to the synecological factors, to understand the pattern and mechanisms for community dynamics of the fragmented secondary forests in sub-urban regions, even though their species composition is largely similar that of old-growth forests.

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Appendix 1 The number (ha^{-1}) of mature individuals, saplings and seedlings**付表-1** 成木、稚樹および実生の密度 (ha^{-1})

Species	Life form ¹⁾	Mature	Saplings	Seedlings ²⁾	Species	Life form ¹⁾	Mature	Saplings	Seedlings ²⁾
<i>Symplocos lucida</i>	EB	174	280	1,317	<i>Zanthoxylum ailanthoides</i>	DB	2	0	103
<i>Castanopsis cuspidata</i>	EB	167	50	885	<i>Aphananthe aspera</i>	DB	2	0	226
<i>Persea thunbergii</i>	EB	98	40	370	<i>Euscaphis japonica</i>	DB	2	15	185
<i>Camellia japonica</i>	EB	84	130	2,572	<i>Symplocos myrtacea</i>	EB	2	0	0
<i>Distylium racemosum</i>	EB	81	95	638	<i>Wisteria floribunda</i>	DB, V	2	0	0
<i>Cornus brachypoda</i>	DB	40	0	800	<i>Viburnum awabuki</i>	EB	2	10	21
<i>Eurya japonica</i>	EB	40	160	432	<i>Ternstroemia gymnanthera</i>	EB	2	5	21
<i>Rhus succedanea</i>	DB	28	0	82	<i>Cinnamomum japonicum</i>	EB	2	10	185
<i>Actinodaphne lancifolia</i>	EB	23	0	82	<i>Aucuba japonica</i>	EB	2	315	*
<i>Ligustrum japonicum</i>	EB	21	70	1,276	<i>Hedera rhombea</i>	EB, V	2	0	0
<i>Daphniphyllum macropodum</i>	EB	16	15	1,564	<i>Cryptomeira japonica</i>	EB	2	0	0
<i>Quercus salicina</i>	EB	14	15	453	<i>Maesa japonica</i>	EN	0	30	*
<i>Styrax japonica</i>	DB	14	5	800	<i>Callicarpa mollis</i>	DB	0	15	412
<i>Cleyera japonica</i>	EB	14	65	103	<i>Acanthopanax sciadophylloides</i>	DB	0	10	0
<i>Trachelospermum asiaticum</i>	EB, V	14	0	*	<i>Prunus spinulosa</i>	EB	0	10	823
<i>var. intermedium</i>					<i>Aralia elata</i>	DB	0	5	0
<i>Premna japonica</i>	DB	12	15	62	<i>Clerodendron trichotomum</i>	DB	0	5	800
<i>Ilex chinensis</i>	EB	9	0	82	<i>Rhododendron kaempferi</i>	DB	0	5	*
<i>Ilex integra</i>	EB	9	25	62	<i>Carpinus tschonoskii</i>	DB	0	0	41
<i>Acer palmatum</i>	DB	7	0	0	<i>Elaeagnus pungens</i>	EB	0	0	41
<i>Dendropanax trifidus</i>	EB	7	30	165	<i>Symplocos prunifolia</i>	EB	0	0	21
<i>Persea japonica</i>	EB	7	10	82	<i>Celtis sinensis</i> var. <i>japonica</i>	EB	0	0	21
<i>Ficus erecta</i>	DB	7	65	267	<i>Diospyros kaki</i>	EB	0	0	21
<i>Actinidia polygama</i>	DB, V	5	0	*	<i>Mallotus japonicus</i>	DB	0	0	21
<i>Neolitsea sericea</i>	EB	5	35	5,391	<i>Rhus javanica</i>	DB	0	0	21
<i>Symplocos glauca</i>	EB	5	10	62	<i>Viburnum erosum</i>	DB	0	0	21
<i>Ilex rotunda</i>	EB	5	150	267	<i>Zanthoxylum piperitum</i>	DB	0	0	21
<i>Actinidia arguta</i>	DB, V	5	0	*	<i>Zanthoxylum schinifolium</i>	DB	0	0	21
<i>Neolitsea aciculata</i>	EB	2	20	494	<i>Euonymus sieboldianus</i>	DB	0	0	21
<i>Platycarya strobilacea</i>	DB	2	0	0					

¹⁾ EB: evergreen broad-leaved species, DB: deciduous broad-leaved species, EN: evergreen needle-leaved species, V: vine.

²⁾ *: species that were not investigated.