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Secondary succession of an unmanaged coppice woodland adjacent to late-successional, lucidophyllous forest in western Japan

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Abstract

The combined effects of management history and ecosystem connectivity make it difficult to predict future dynamics of abandoned, unmanaged ecosystems. In Japan, unmanaged, secondary forests (*satoyama*) face risk of arrested or diverted succession, due to extensive human influence across the landscape. Proximity to climax forests, which function as seed sources could determine the course of succession of abandoned satoyama. Here, we investigated spatial/temporal variation of species composition and stand structure of abandoned satoyama adjacent to a mature lucidophyllous forest in warm-temperate Japan to elucidate the course of succession after abandonment. Two study plots were established in the unmanaged, secondary forest at varying distances from the mature lucidophyllous forest. We calculated vegetation similarity indices among the plots to elucidate spatial variation and temporal change of species composition and stand structure and visualized relationships using nMDS (non-metric multidimensional scaling) ordination. Over the past 15 years, species composition and stand structure of the secondary forest changed following the normal sere of succession. This was because shade-intolerant shrubs, such as *Rhododendron* were replaced by recruitment of climax species originating from the lucidophyllous forest. However, *Quercus serrata* (deciduous oak) and shade-intolerant evergreen trees continued to dominate the upper-canopy. Although the adjacent lucidophyllous forest is an effective seed source for recruitment of climax species, it may take several decades for the secondary forest to reach late-successional composition and structure, due to legacy effects of past management.

Keywords: traditional forest management, legacy effects, plagiosere, forest fragmentation, recruitment limitation

Introduction

Traditional agricultural landscapes are rapidly disappearing due to socio-economic changes and modernization (Agnoletti 2007; Dobrovodská et al. 2019). However, effects of past land management practices (legacy effects) can persist for decades to centuries after traditional practices are abandoned, influencing the subsequent trajectory of ecosystem dynamics, such as vegetation succession, carbon stocks, nutrient cycling, etc. (Foster et al. 2003; Hermy and Verheyen 2007). In addition, as human-domination of the landscape proceeds, natural ecosystems become more fragmented, negatively influencing landscape-scale ecosystem processes such as metapopulation dynamics and forest succession (Baiamonte et al. 2015; Duelli and Obrist 2003; Martín-Queller and Saura 2013). The combined effects of ecological history and ecosystem connectivity complicates succession and dynamics of abandoned, unmanaged ecosystems (Foster et al. 2003).

Satoyama are secondary forests traditionally managed under coppice forestry to obtain firewood, organic fertilizer and other forest resources in the traditional agricultural landscape of Japan (Morimoto 2011; Takeuchi et al. 2003; Yokohari and Bolthouse 2011). Recent research has shown that traditional agricultural management associated with satoyama landscapes maintains a mosaic of forests at various stages of succession (Iwachido et al. 2020; Katoh et al. 2009; Yamasaki et al. 2000). Traditionally, coppice management had prevented succession of satoyama to climax forest (Kobori and Primack 2003) and maintained open forests at early stages of succession dominated by shade-intolerant species (Nagaike et al. 2003; Takeuchi 2010). Traditional agricultural landscapes in Japan are rapidly disappearing (Takeuchi 2010; Washitani 2001). Many satoyama forests in Japan were abandoned in the 1960-70s as firewood and organic fertilizer were replaced by fossil fuel and chemical fertilizer (Jiao et al. 2019). Thus these secondary forests have been unmanaged for 50-60 years and are now in mid-succession.

In warm-temperate Japan, the unmanaged forests are transitioning from dominance by shade-intolerant, deciduous broad-leaved trees (e.g., *Quercus variabilis*, *Quercus serrata*) to increasing abundance of shade-tolerant, evergreen broadleaved trees invading the understory and shrub layers (Hirayama et al. 2011; Ito 2007; Nakajima et al. 2018). Similar dynamics are observed in abandoned coppice-managed woodlands in Europe (Douda et al. 2017; Hedl et al. 2010; e.g.,Keith et al. 2009). In warm-temperate Japan, unmanaged secondary forests are expected to succeed to lucidophyllous forest, the potential climax vegetation (Miyawaki 2004; Nakagoshi and Hong 2001; Nakajima et al. 2018). However, recruitment limitation due to lack of seed sources could arrest vegetation dynamics at mid-succession (e.g., Acácio et al. 2007). Furthermore, invasion by non-native species could divert the course of vegetation succession (plagiosere, Moriyama et al. 1984; Tojima et al. 2004). The future course of succession of unmanaged secondary forests to potential climax vegetation, therefore, is uncertain.

Because of extensive human influence across the landscape, climax forests are rare globally (Rackham 2008). In warm-temperate Japan, the few climax forests in populated areas are preserved in shrines and temples, for purposes of religious worship (Kamada 2005; Ishii et al. 2010). Such forests are rare specimens of the potential climax vegetation (Miyawaki 1998), and could function as seed sources of climax species. Here, we investigated spatio-temporal variation in species composition and stand structure of an unmanaged secondary forest adjacent to a preserved lucidophyllous forest at a temple in western Japan. Observations indicated that the secondary forest, which has been unmanaged for nearly 60 years, is being invaded by shade-tolerant, evergreen species originating from the lucidophyllous forest. This has resulted in a spatial gradient of successional stages with increasing distance from the lucidophyllous forest (Azuma et al, 2014). To take advantage of this unique setting, we established research plots along this spatial gradient to investigate spatial variation in species composition and stand structure as well as temporal change over 15 years. Our objective was to elucidate the course of succession of abandoned satoyama to lucidophyllous forest in warm-temperate Japan.

Study Site and Methods

The study was conducted in an unmanaged secondary forest and adjacent lucidophyllous forest at Taisanji Temple, Hyogo Prefecture, Japan (34°41′N, 135°04′E, 70–200 m ASL, Fig. 1). The substrate of the slopes surrounding Taisanji Temple is granite (Kodate and Nakanishi 1986). Historical drawings from 1803 suggest that the surrounding vegetation was open pine forest (Matsushita 1997). Vegetation maps and survey data from 1960-1970 indicate evergreen forests had established surrounding the temple grounds suggesting succession had proceeded (Kodate and Nakanishi 1986). The evergreen forest, directly behind the temple grounds, is a place of Buddhist training and has had minimal human intervention. The mature lucidophyllous forest is dominated by *Castanopsis cuspidata* and comprises many indigenous species, representative of climax forest in this region (Ishida et al. 1998). Adjacent to the mature lucidophyllous forest is unmanaged secondary forest (abandoned satoyama), where neighboring farmers had actively utilized the forest until ca. 1960s. The secondary forest is dominated by deciduous broad-leaved trees. Observations suggest, after management ceased, evergreen trees from the lucidophyllous forest are slowly invading into the secondary forest creating a spatial gradient of forest succession with increasing distance from the lucidophyllous forest.

We established two permanent plots to observe vegetation dynamics. The mature lucidophyllous forest (M) plot (50x50 m) was established in 2003 at the foot of the hill on the temple side, while the far-secondary forest (F) plot (50x40 m) was established in 2005 in the unmanaged secondary forest on the opposite side of the hill (Fig 1). These plots are the same as those studied by Azuma et al. (2014). We counted approximately 100 annual rings in a core sample taken at 30 cm height from the trunk of the largest tree in the M plot in 2012 (*C. cuspidata*, DBH=78 cm), suggesting the forest is near climax stage. In the F plot, we counted 60-70 annual rings from core samples from the stems of multi-stemmed *Quercus serrata* and *Quercus variabilis* trees, suggesting the secondary forest was last cut around 1950 (Azuma et al. 2014). We measured diameter at breast height (DBH, 1.3 m above ground) and height of all trees taller than 1.3 m within the research plots using diameter tapes, digital calipers (for DBH < 2 cm), telescoping poles (height < 8 m), and ultra-sound clinometers

(Vertex III, Haglof, Sweden). Diameter measurements were repeated in 2008, 2014 and 2020. Height measurements were repeated in 2014 and 2020. These two plots were used to observe temporal change in species composition and stand structure.

In 2020, we established two additional research plots near the ridge of the hill between the M and F plots to investigate spatial variation of species composition and stand structure with increasing distance from the mature lucidophyllous forest. The young lucidophyllous forest (Y) plot (20x30 m) is located in a relatively young lucidophyllous forest ca. 100 m upslope from the M plot (Fig. 1). The close-secondary (C) forest plot (20x40 m) is located in a mixed evergreen-deciduous forest on the mature forest side, upslope of the F plot. Plot sizes are variable reflecting the spatial extent of each forest type. We counted 48-65 annual rings in core samples taken at 30 cm height from trunk of the largest trees in the Y and C plots (all *C. cuspidata*), indicating that the Y plot is younger than the M plot and that the oldest *C. cuspidata* trees established in the C plot soon after management ceased. DBH and tree height of all trees taller than 1.3 m in Y and C plots were measured using the same criteria and methods as for the M and F plots above.

Data analysis

Using the DBH data in each survey year, we calculated basal area (BA, m^2 ha^{-1}) for each tree species in the plots. We used the Chao-Jaccard index to compare species composition among the plots based on abundance (trees ha^{-1}) and the Bray-Curtis index to compare stand structure based on BA. We chose

Chao-Jaccard over the Bray-Curtis index for abundance because the Bray-Curtis index is heavily influenced by the relative abundance of species. The Bray-Curtis index can be calculated based on relative abundance of species (e.g., De Caceres et al. 2013; Hao et al, 2019), indicating that the independent variables need not be count data. Several previous studies have applied the Bray-Curtis index to assess similarity in stand structure among communities using relative basal area (e.g., La Torre-Cuadros et al, 2007; Hotta et al, 2015; Sasaki et al. 2018).

The results were visualized using non-metric multidimensional scaling (nMDS) ordination using the function “metaMDS” of the package “vegan” in R software (ver. 3.4.1, R Development Core Team) (Oksanen et al. 2020). The nMDS is a distance-based ordination technique where relationships among biological communities are drawn on a two-dimensional plane to display graphically similarities among ecological communities. It is suited for ecological analyses because it is nonparametric and can be used to relativize distance measures based on a wide variety of ecological data (McCune et al. 2002). Distance between plots on the nMDS ordination plane represent their relative similarities. Here, changes over time of the coordinates of the F plot relative to the M plot on the nMDS ordination plane was interpreted as the course of succession (Hiers et al. 2012; Mathews et al. 2010; Ruiz-Jaen and Aide 2006). We used type-two permutational multivariate analysis of variance (PERMANOVA) using distance matrices and evaluated plot distances on the nMDS plane to test significant change over time and differences among plots in species composition and stand structure, respectively. PERMANOVA (9999 permutations) was conducted using the function “adonis2” of the "vegan" package in R. Multiple comparisons for evaluating distances between plots were conducted using the "pairwiseAdonis2" package, where p-values of the pairwise PREMANOVA are corrected using the Holm correction (Hervé 2016). In addition to visualizing similarity among communities, correlations between the original species vectors, abundance/dominance of a species in each community, and the axis scores of the nMDS ordination can be computed and these correlations scaled to represent the direction and strength of influence of species on each community (Legendre and Gallaghar 2001). To infer species that affected composition and structure of the study plots, we plotted species having significant correlations with axes 1 and 2 on the nMDS ordination plane.

Results

Temporal change of species composition and stand structure

Comparison of DBH distributions between 2003 and 2014 indicated that species composition and size distribution of the M plot had changed very little between surveys and was characterized by dominance of shade-tolerant, climax species, such as *C. cuspidata*, *Aucuba japonica*, *Camellia japonica* and *Cleyera japonica* (Fig. 2). In contrast, species composition of the F plot in 2005 was characterized by dominance of shade-intolerant, deciduous (e.g., *Q. serrata*, *Lyonia ovallifolia*) and evergreen (e.g., *Ilex pendiculosa*, *Quercus phillyraeoides*) trees and deciduous shrubs (e.g., *Rhododendron reticulatum*). While stem density remained relatively stable in both plots (ca. 2400 and 3800 trees ha^{-1}, for M and F plots, respectively, Table S1, S2), total BA increased by 22% (from 37.11 m^2 ha^{-1} in 2003 to 45.27 in

2020) in the M plot and by 37% (21.66 m^2 ha^{-1} in 2003 to 29.67 in 2020) in the F plot (Table S3, S4).

Comparison of height distributions between 2003 and 2014 indicated that canopy height of the M plot increased, but the relative vertical distribution of species remained stable (Fig. 2). The upper canopy continued to be dominated by *C. cuspidata*, which had the largest BA (Table S3), and the lower canopy by *Camellia japonica*. Canopy height of the F plot also increased. While *Q. serrata* continued to dominate in the upper-canopy as well as in BA (Table S4), marked changes were observed in the vertical distribution of species in the mid- and lower-canopy layers. *Q. phillyraeoides* and *Ilex pedunculosa* increased markedly in height and BA and dominated the mid-canopy in 2014, while in the lower canopy, deciduous species (e.g., *R. reticulatum, L. ovafolia*) decreased and evergreen species (e.g., *Camellia japonica*, *Cleyera japonica*) increased.

Abundances of the dominant climax species in the M plot were positively correlated with Axis 1 and negatively correlated with Axis 2 of the abundance-based nMDS ordination plane, while it was vice versa for the dominant species of the F plot (Fig. 3). The BA of *C. cuspidata* was positively correlated, while that of the dominant species in the F plot was negatively correlated with Axis 1 of the BA-based nMDS ordination plane. During the study period, the coordinates of the M plot changed very little in relation to Axis 1 of both the abundance- and BA-based nMDS, reflecting stable species composition and stand structure. In contrast, Axis 1 values of the F plot tended to increase toward the direction of the M plot, although these changes were not statistically significant (Table 1, 2).

Spatial variation with distance from mature forest

Results of the most recent survey in 2020 indicated that the M and Y plots were dominated by *C. cuspidata* with *Camellia japonica* and other evergreen species comprising the mid- to lower-canopy layers (Fig. 4). The DBH and height of *C. cuspidata* in the Y plot were smaller than in the M plot, reflecting the difference in stand age. Compared to the F plot, where the upper-canopy and BA were both dominated by *Q. serrata*, *C. cuspidata* dominated the upper-canopy of the C plot and evergreen species contributed larger proportion of the total BA (Table S6). The mid-canopy layer was more developed in the C plot, where *I. pedunculosa*, *Q. phillyraeoides* and *Clethra barbinervis* dominated in the mid-DBH (10-20 cm) and mid-height (7.3-13.3 m) classes. Shade-intolerant deciduous species (*R. reticulatum*, *L. ovalifolia*) were less abundant in the lower-canopy layer of the C plot.

Abundance-based nMDS indicated that species compositions of the M and Y plots were very similar to each other (Fig. 5, Table 3). Species composition of the F and C plots were different from the M and Y plots, as well as from each other. BA-based nMDS indicated that, stand structure of the M and Y plots differed from each other, reflecting the difference in size distribution of the dominant species (Table 4). Stand structure of the F and C plots differed from M and Y plots, as well as from each other, reflecting the difference in vertical distribution of species.

Discussion

Our results indicated that, in contrast to the dynamic changes observed in the far-secondary forest during the study period, species composition and stand structure of the mature lucidophyllous forest remained relatively stable, suggesting it is approaching climax state. In the far-secondary forest, shade-intolerant species, such as *R. reticulatum* and *L. ovalifolia*, decreased markedly in the lower-canopy layer during the study period and were replaced by shade-tolerant evergreen species. Similar vegetation dynamics have been observed in unmanaged secondary forests in many regions in Japan (Nakajima et al. 2018). For example, in an unmanaged, secondary broad-leaved forest in Kyoto, tree density decreased over a 12-year period as shade-intolerant shrubs were replaced by evergreen species such as *Cleyera japonica* and *E. japonica*, whereas total basal area increased due to growth of the canopy dominant trees (Ito 2007). Hirayama et al. (2011) compared species composition between mid-successional forest dominated by *Q. serrata* and *Q. variabilis* (abandoned satoyama), with that of a late-successional forest dominated by *C. cuspidata*, and found that the former had a more developed shrub layer. Morimoto and Yoshida (2005) found that between 1974 and 1995, native *Rhododendron* populations in Kyoto city had declined as the number of unmanaged secondary forests increased. Traditional coppice management maintained the forests at early stages of succession with open canopy conditions (Kobori and Primack 2003). Our results together with reports from other unmanaged satoyama across Japan suggest that, after management ceased, growth and increasing leaf area of the upper-canopy trees reduce the amount of light penetrating into the forest such that, in the lower-canopy, shade-intolerant species gradually decline and are replaced by shade-tolerant evergreen species.

In warm-temperate Japan, the dominant canopy species are expected to succeed from shade-intolerant, deciduous oaks to shade-tolerant, evergreen oaks (Miyawaki 2004). Seeds of these Fagaceous species (acorns) are mostly gravity and animal dispersed. In secondary forests in Japan, acorns may be transported 20 m to as much as 40 m by rodents (Iida 1996). Birds can also transport *C. cuspidata* acorns over long distances (Hiroki 2001). In a secondary forest dominated by *Q. variabilis* and *Q. serrata*, continuous recruitment and gradual invasion of *C. cuspidata* into the secondary forest occurred, such that seedlings of *C. cuspidata* established as far as 40 m away from the nearest adult trees in the adjacent *C. cuspidata*–dominated forest (Hirayama et al. 2010). Our results indicated evergreen trees and shrubs, originating from the lucidophyllous forest are invading the lower-canopy of the secondary forest. The direction of temporal change on the nMDS ordination plane suggested that the secondary forest is succeeding toward the climax, lucidophyllous forest following the normal sere for warm-temperate Japan. The marked difference in canopy structure between the mature and secondary forests, however, indicated seedlings and young trees of *C. cuspidata* in the lower canopy of the secondary forest are far from attaining dominant status, because deciduous oaks and shade-intolerant evergreen trees continue to dominate the upper canopy. Slope position may also affect stand growth and management history. Growth of *C. cuspidata* may be slower in the upper-slope stands (Y and C plots). Because of its lower-slope position (i.e., ease of access), the F plot may have been managed more frequently than the C plot, maintaining the far-secondary forest at early-successional stage until more recently.

Conclusions

Spatio-temporal analysis of species composition and stand structure of unmanaged, secondary forest adjacent to mature lucidophyllous forest using nMDS ordination allowed us to infer the course of succession of unmanaged satoyama. Past management practices, such as coppice forestry in the case of satoyama, may continue to influence composition and structure of ecosystems for decades to centuries (Bürgi et al. 2013; Douda et al. 2017; Perring et al. 2016). In addition, connectivity, seed flux, and colonization among different communities within a landscape influence species composition (Martín-Queller and Saura 2013). The lack of source populations in human-dominated landscapes can cause recruitment limitation arresting vegetation dynamics at mid-succession (Acácio et al. 2007; Duelli and Obrist 2003). Remnants of natural and semi-natural habitats can function as refugia for rare species and as stepping stones for species dispersal, contributing to restoration of inherent vegetation dynamics at the landscape level (Duelli and Obrist 2003). Although dynamic changes in species composition, especially in the lower-canopy, have been observed in many unmanaged satoyama, our results suggested legacy effects of satoyama management can persist for several decades before individual canopy trees are replaced by natural disturbances such as typhoon, and the unmanaged secondary forest attains climax composition and structure. In this study, the adjacent lucidophyllous forest acted as a seed source for recruitment of shade-tolerant species into the unmanaged, secondary forest. However, for secondary forests which lack nearby seed sources of climax species, close monitoring of vegetation change may be necessary to prevent arrested or diverted succession. Further studies should elucidate dynamics of unmanaged satoyama in the context of landscape-level distribution of natural and semi-natural forests.

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Author contributions

HI conceived and designed the study. Fieldwork and data collection was led by NK with assistance from TY, KH, and WAA. TY and NK analyzed the data together and prepared all figures. HI wrote the first draft of the manuscript. All authors have approved the final manuscript.

Declarations

Ethical Approval

Not applicable

Competing interests

None declared.

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Availability of data and materials

Data will be made available in the Kobe University data repository upon acceptance.

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Table 1. Temporal change of species composition as measured by pairwise Chao-Jaccard similarity indices based on abundance of species.

Plot		Mature lucidophyllous			Far Secondary			
	Year	2008	2014	2020	2005	2008	2014	2020
M	2003	0.066	0.096	0.118	0.889**	0.879**	0.867**	0.860**
	2008		0.037	0.057	0.897**	0.887**	0.876**	0.869**
	2014			0.026	0.896**	0.887**	0.876**	0.868**
	2020				0.899**	0.890**	0.879**	0.871**
F	2005					0.070	0.117	0.167
	2008						0.067	0.106
	2014							0.055

**: P < 0.01, Larger values reflect lower similarity.

Table 2. Temporal change of stand structure as measured by pairwise Bray-Curtis similarity indices based on basal area of species.

Plot		Mature lucidophyllous			Far Secondary			
	Year	2008	2014	2020	2005	2008	2014	2020
M	2003	0.118	0.170	0.168	0.816**	0.809**	0.782**	0.754**
	2008		0.094	0.114	0.822**	0.814**	0.787**	0.762**
	2014			0.072	0.823**	0.815**	0.787**	0.761**
	2020				0.826**	0.818**	0.790**	0.764**
F	2005					0.082	0.194	0.268
	2008						0.157	0.240
	2014							0.122

**: P < 0.01, Larger values reflect lower similarity.

Table 3. Spatial variation of species composition as measured by pairwise Chao-Jaccard similarity indices based on abundance of species.

Plot	Y	C	F
M	0.341	0.651**	0.871**
Y		0.577*	0.823**
C			0.515*

M: mature lucidophyllous; Y: young lucidophyllous; C: close-secondary; F: far-secondary plots.
*: P <0.05; **: P < 0.01, Larger values reflect lower similarity.

Table 4. Spatial variation of species composition as measured by pairwise Bray-Curtis similarity indices based on basal area of species.

Plot	Y	C	F
M	0.535*	0.739**	0.764**
Y		0.746**	0.770**
C			0.588**

M: mature lucidophyllous; Y: young lucidophyllous; C: close-secondary; F: far-secondary plots.
*: P<0.05; **: P < 0.01, Larger values reflect lower similarity.

Figure captions

Fig. 1. Location of the study site, Taisanji Temple, in Kobe City, Japan (a). The mature lucidophyllous forest is located on the west side of the mountain (b, solid outline). The east side of the ridge-line is secondary forest, which was cut regularly to obtain fire-wood until ca. 60 years ago, after which it was abandoned (b, dotted outline). Climax species originating from the lucidophyllous forest are invading into the secondary forest. Four study plots were established along the spatial gradient of vegetation change with increasing distance from the mature lucidophyllous forest: mature lucidophyllous (M), young lucidophyllous (Y), close-secondary (C), and far secondary (F) plots.

Fig. 2. Temporal change of diameter and height distributions of species in the mature lucidophyllous and far-secondary forest plots during the study period. The bars for the smallest diameter/height classes in each plot are truncated and numbers next to the bars indicate number of trees.

Fig. 3. Nonmetric multidimensional scaling (nMDS) ordination of vegetation similarity based on abundance and basal area of the mature lucidophyllous (M, □) and the far secondary (F, O) plots during the study period. Coordinates of each species (+: deciduous, X: evergreen) reflect correlations with each nMDS axis. Stress values are < 0.01 for both abundance and basal area.

Fig. 4. Diameter and height distributions of species in the four research plots in 2020. The bars for the smallest diameter/height classes in each plot are truncated and numbers next to the bars indicate number of trees.

Fig. 5. Nonmetric multidimensional scaling (nMDS) ordination of vegetation similarity based on abundance and basal area of the mature lucidophyllous (M, □), young lucidophyllous (Y, ◊), far secondary (F, O) and close-secondary (C, Δ) plots in 2020. Coordinates of each species (+: deciduous, X: evergreen) reflect correlations with each nMDS axis. Stress values are less than 0.01 for both abundance and basal area.

Fig 1

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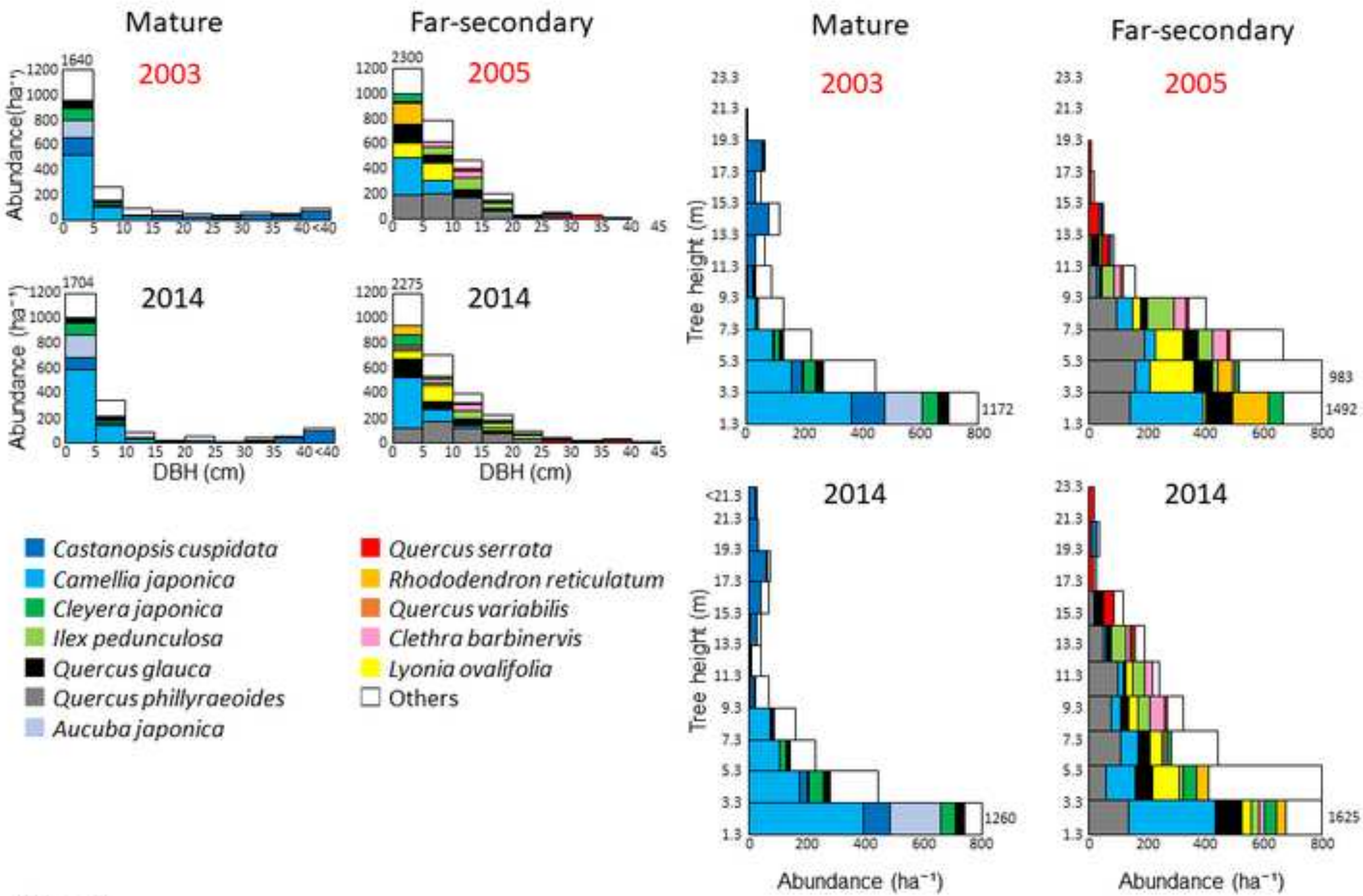

Fig 2

Figure 3

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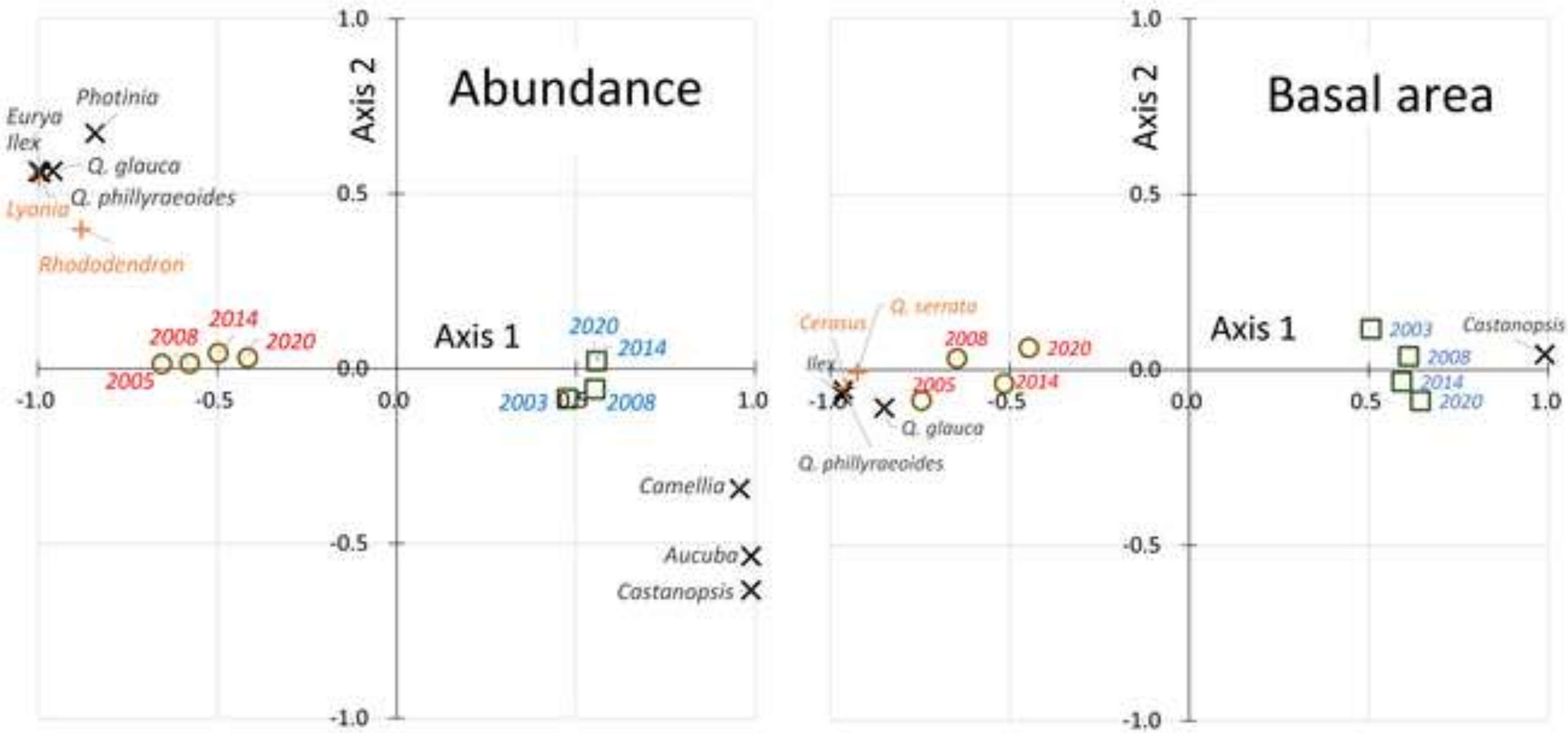

Fig 3

Figure 4

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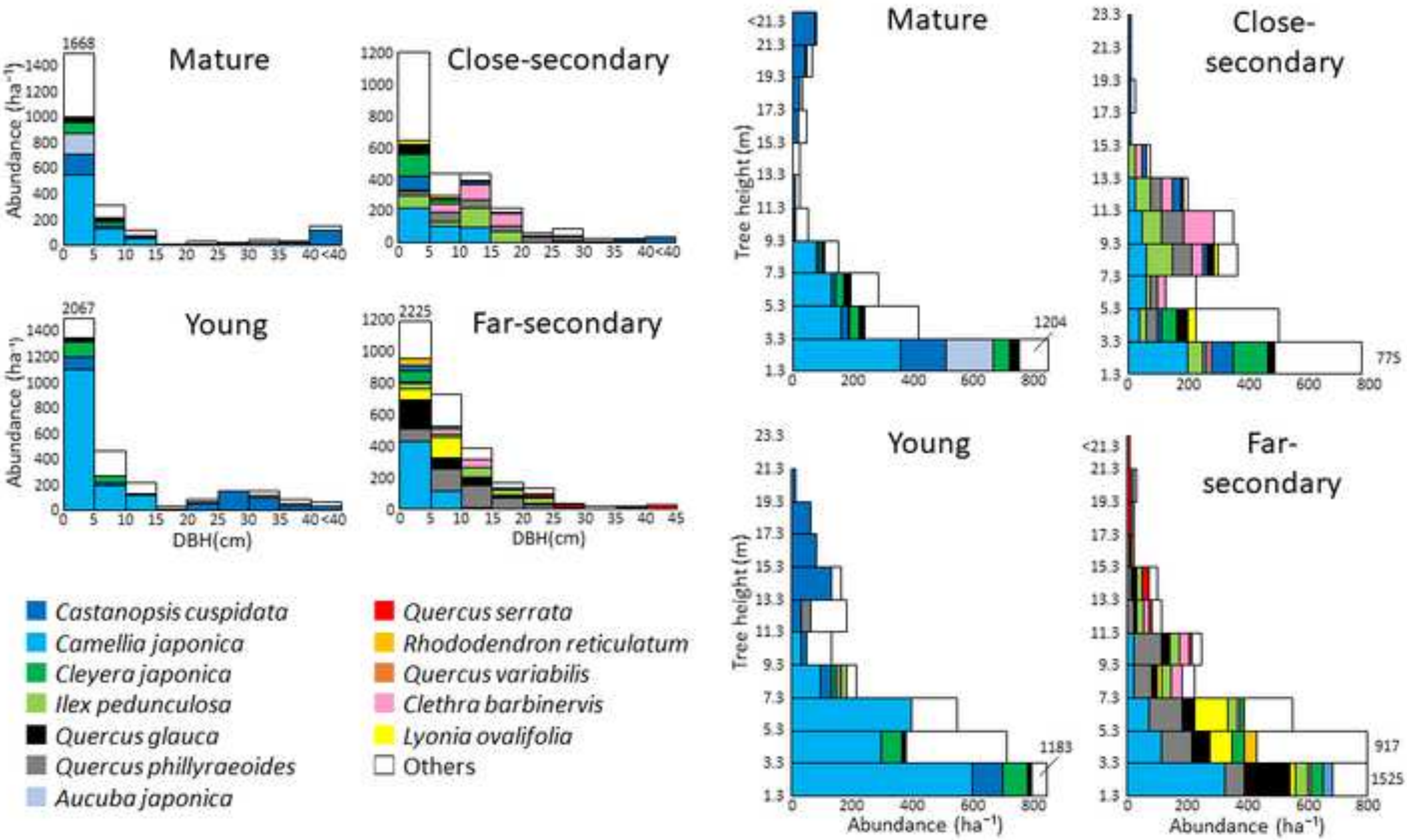

Fig 4

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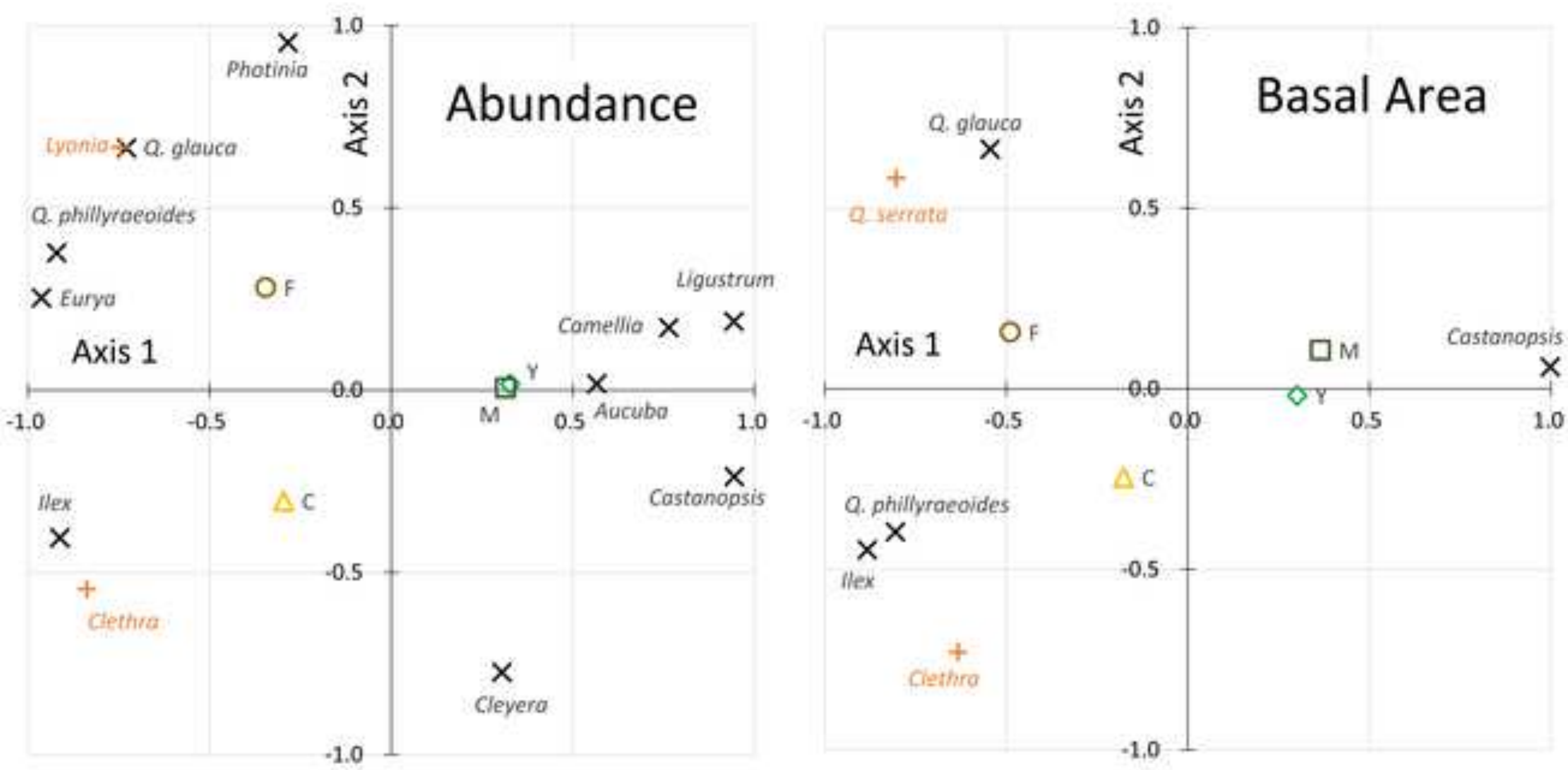

Fig 5

Table S1. Species composition of the mature lucidophyllous forest (M) plot. Species are listed in order of decreasing abundance in the first survey year. Bold letters indicate evergreen species.

Mature lucidophyllous forest	Abundance(ha⁻¹)			
Species	2003	2008	2014	2020
Camellia japonica	656	740	764	744
Castanopsis cuspidata	384	360	328	372
Eurya japonica	164	176	156	144
Ligustrum japonicum	164	164	140	112
Aucuba japonica	136	176	176	160
Cleyera japonica	116	132	124	124
Quercus glauca	96	92	88	88
Photinia glabra	72	84	100	108
Ilex rotunda	68	80	80	76
Dendropanax trifidus	52	52	48	44
Distylium racemosum	48	56	64	64
Ilex integra	48	64	60	56
Aphananthe aspera	36	56	44	44
Cinnamomum yabunikkei	36	48	48	40
Ficus erecta	36	32	32	32
Ilex chinensis	28	28	20	16
Quercus salicina	24	16	8	4
Callicarpa mollis	20	24	12	16
Symplocos prunifolia	20	16	16	8
Litsea coreana	16	16	20	20
Magnolia compressa	12	12	12	12
Zanthoxylum ailanthoides	12	12	12	12
Platycarya strobilacea	12	12	12	12
Laurocerasus spinulosa	12	12	8	8
Elaeagnus glabra	8	28	20	20
Ternstroemia gymnanthera	8	8	8	8
Osmanthus heterophyllus	8	8	8	8
Gardenia jasminoides var. jasminoides	8	8	8	8
Celtis sinensis	8	8	4	4
Carpinus laxiflora	8	8	4	0
Daphniphyllum teijsmannii	4	4	4	4
Nandina domestica	4	4	4	4
Elaeagnus pungens	4	4	4	4
Machilus thunbergii	4	4	0	0
Neolitsea aciculata	4	4	0	0
Rapanaea neriifolia	4	4	0	0
Plotosus japonicus	4	0	0	0
Zelkova serrata	4	4	4	0
Fraxinus sieboldiana	4	4	0	0
Ilex pedunculosa	4	0	0	0
Euonymus sieboldianus	4	4	0	0
Sambucus racemosa	0	0	4	8
Callicarpa japonica	0	4	4	4
Total	2360	2568	2448	2388

Table S2. Species composition of the far secondary forest (F) plot. Species are listed in order of decreasing abundance in the first survey year. Bold letters indicate evergreen species.

Far secondary forest	Abundance(ha^{-1})			
Species	2005	2008	2014	2020
Quercus phillyraeoides	617	600	542	475
Eurya japonica	583	633	617	558
Camellia japonica	400	442	517	567
Lyonia ovalifolia	283	275	225	217
Quercus glauca	267	250	267	317
Photinia glabra	208	242	350	367
Ilex pedunculosa	208	208	192	183
Rhododendron reticulatum	175	108	75	42
Eleutherococcus innovans	142	133	108	100
Clethra barbinervis	125	125	117	100
Fraxinus sieboldiana	125	108	83	92
Quercus serrata	92	92	92	92
Osmanthus heterophyllus	83	100	83	100
Cleyera japonica	67	67	100	100
Abelia spathulata	67	67	25	0
Cerasus leveilleana	58	58	50	50
Dendropanax trifidus	42	42	42	42
Viburnum erosum	42	42	17	17
Rhododendron macrosepalum	33	50	42	33
Rhododendron serpyllifolium	33	33	17	8
Pourthiaea villosa	25	25	25	25
Quercus salicina	25	25	17	17
Castanopsis cuspidata	17	17	17	50
Ligustrum japonicum	17	17	17	25
Symplocos prunifolia	17	17	17	25
Vaccinium bracteatum	17	17	17	17
Carpinus laxiflora	17	17	17	17
Viburnum wrightii	17	8	33	8
Daphniphyllum teijsmannii	8	17	17	42
Ilex rotunda	8	8	8	17
Callicarpa mollis	8	8	8	8
Ternstroemia gymnanthera	8	8	8	8
Aria japonica	8	17	8	8
Carpinus tschonoskii	8	8	8	8
Quercus variabilis	8	8	8	8
Ilex crenata	0	8	17	17
Abelia serrata	0	0	8	8
Symplocos kuroki	0	0	8	8
Quercus myrsinifolia	0	8	0	0
Total	3858	3908	3817	3775

Table S3. Stand structure of the mature lucidophyllous forest (M) plot. Species are listed in order of decreasing basal area in the first survey year. Bold letters indicate evergreen species.

Mature lucidophyllous forest	BA(m^2 ha^{-1})			
Species	2003	2008	2014	2020
Castanopsis cuspidata	26.04	29.74	30.97	31.42
Platycarya strobilacea	1.59	1.77	1.99	2.28
Ilex integra	1.41	1.56	1.76	1.99
Camellia japonica	1.19	1.37	1.38	1.55
Celtis sinensis	0.91	1.03	0.59	0.64
Quercus glauca	0.80	0.84	0.97	1.06
Zanthoxylum ailanthoides	0.72	0.81	0.87	0.97
Ilex rotunda	0.71	0.82	0.86	0.99
Daphniphyllum teijsmannii	0.59	0.70	0.84	0.91
Quercus salicina	0.56	0.61	0.49	0.63
Litsea coreana	0.52	0.60	0.64	0.74
Dendropanax trifidus	0.41	0.45	0.36	0.32
Symplocos prunifolia	0.34	0.25	0.28	0.18
Ligustrum japonicum	0.25	0.29	0.27	0.22
Ilex chinensis	0.17	0.18	0.23	0.27
Cinnamomum yabunikkei	0.16	0.17	0.14	0.14
Distylium racemosum	0.15	0.16	0.14	0.15
Cleyera japonica	0.11	0.14	0.17	0.21
Machilus thunbergii	0.10	0.10	0.00	0.00
Laurocerasus spinulosa	0.08	0.09	0.00	0.00
Photinia glabra	0.06	0.08	0.09	0.12
Eurya japonica	0.06	0.08	0.08	0.08
Carpinus laxiflora	0.05	0.05	0.02	0.00
Aphananthe aspera	0.04	0.08	0.16	0.29
Magnolia compressa	0.04	0.04	0.05	0.05
Ficus erecta	0.02	0.03	0.03	0.03
Aucuba japonica	0.02	0.02	0.03	0.02
Fraxinus sieboldiana	0.01	0.02	0.00	0.00
Gardenia jasminoides var. jasminoides	0.01	0.01	0.01	0.01
Others	0.01	0.01	0.01	0.01
Total	37.11	42.10	43.42	45.27

Table S4. Stand structure of the far secondary forest (F) plot. Species are listed in order of decreasing basal area in the first survey year. Bold letters indicate evergreen species.

Far secondary forest	BA($m^2 ha^{-1}$)			
Species	2005	2008	2014	2020
Quercus serrata	4.96	5.67	6.67	7.99
Quercus phillyraeoides	4.47	5.18	5.50	5.71
Ilex pedunculosa	2.73	2.95	3.24	3.34
Cerasus leveilleana	1.36	1.55	1.72	1.81
Quercus glauca	1.20	1.43	1.24	1.49
Clethra barbinervis	1.16	1.26	1.11	1.16
Lyonia ovalifolia	1.10	1.16	1.01	0.91
Castanopsis cuspidata	0.95	1.14	1.40	1.59
Eleutherococcus innovans	0.57	0.60	0.53	0.58
Camellia japonica	0.48	0.58	0.74	0.80
Symplocos prunifolia	0.43	0.65	0.59	0.63
Quercus variabilis	0.41	0.49	0.65	0.81
Quercus salicina	0.36	0.42	0.36	0.42
Eurya japonica	0.33	0.38	0.39	0.41
Carpinus laxiflora	0.30	0.32	0.32	0.33
Photinia glabra	0.19	0.25	0.33	0.47
Aria japonica	0.11	0.12	0.12	0.13
Carpinus tschonoskii	0.10	0.11	0.15	0.18
Fraxinus sieboldiana	0.09	0.08	0.09	0.08
Osmanthus heterophyllus	0.07	0.08	0.04	0.04
Rhododendron reticulatum	0.06	0.04	0.05	0.03
Daphniphyllum teijsmannii	0.06	0.12	0.17	0.24
Dendropanax trifidus	0.05	0.11	0.14	0.16
Cleyera japonica	0.04	0.06	0.11	0.15
Vaccinium bracteatum	0.03	0.03	0.03	0.03
Ternstroemia gymnanthera	0.02	0.03	0.07	0.08
Ligustrum japonicum	0.01	0.01	0.01	0.02
Pourthiaea villosa	0.01	0.01	0.01	0.01
Abelia spathulata	0.01	0.03	<0.01	<0.001
Other	0.01	0.02	0.04	0.05
Total	21.66	24.86	26.85	29.67

Table S5. Species composition and stand structure of the young lucidophyllous forest (Y) plot in 2020. Species are listed in order of decreasing basal area. Bold letters indicate evergreen species.

Young lucidophyllous	2020	
Species	Abundance (ha^{-1})	BA ($m^2 ha^{-1}$)
Castanopsis cuspidata	483	28.77
Quercus myrsinifolia	100	4.36
Quercus phillyraeoides	50	3.87
Ilex integra	50	3.64
Camellia japonica	1433	3.28
Myrica rubra	17	2.18
Diospyros kaki	33	1.79
Carpinus laxiflora	17	1.76
Dendropanax trifidus	150	0.74
Ligustrum japonicum	167	0.33
Ilex pedunculosa	17	0.23
Ternstroemia gymnanthera	117	0.22
Cleyera japonica	167	0.21
Photinia glabra	150	0.20
Cinnamomum yabunikkei	67	0.20
Eurya japonica	183	0.13
Ilex rotunda	17	0.12
Symplocos prunifolia	17	0.07
Quercus glauca	33	0.01
Osmanthus heterophyllus	50	0.00
Total	3317	52.11

Table S6. Species composition and stand structure of the close secondary forest (C) plot in 2020. Species are listed in order of decreasing basal area. Bold letters indicate evergreen species.

Close secondary forest	2020	
Species	Abundance (ha^{-1})	BA (m^2 ha^{-1})
Camellia japonica	438	10.63
Eurya japonica	413	5.70
Ilex pedunculosa	313	4.23
Quercus phillyraeoides	250	3.03
Clethra barbinervis	238	2.32
Castanopsis cuspidata	188	1.57
Cleyera japonica	163	1.10
Symplocos prunifolia	138	0.78
Quercus glauca	100	0.46
Eleutherococcus innovans	50	0.41
Lyonia ovalifolia	38	0.31
Osmanthus heterophyllus	38	0.23
Pourthiaea villosa	38	0.17
Quercus myrsinifolia	25	0.15
Photinia glabra	13	0.12
Dendropanax trifidus	13	0.10
Daphniphyllum teijsmannii	13	0.07
Myrica rubra	13	0.02
Fraxinus lanuginosa	13	0.01
Styrax japonicus	13	0.01
Viburnum dilatatum	13	<0.01
Cerasus sargentii	13	<0.01
Rhododendron albiflorum	13	<0.01
Rhus succedanea	13	<0.01
Total	2550	31.42