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# The spatio-temporal pattern of historical disturbances of an evergreen broadleaved forest in East China: a dendroecological analysis

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**Abstract** Evergreen broadleaved forests (EBLF), the zonal forest ecosystem of the subtropical zone in east China, have been degraded from recent anthropogenic disturbance. Understanding the role of past disturbances in EBLFs would be helpful to the restoration of degraded EBLFs. We used dendroecological techniques to reconstruct the disturbance history of a secondary EBLF dominated by *Schima superba* and *Castanopsis carlesii* in Tiantong National Forest Park (29°48′N, 121°47′E), Zhejiang Province, East China. The disturbances were inferred from tree-ring growth release and long-term establishment patterns obtained from 91 overstory trees. The initial growth rates of these trees were compared to trees originating in the understory to evaluate the intensity of past disturbances. The spatial distribution patterns of disturbances were portrayed with tree mapping. The results revealed that there were five disturbances, averaging one disturbance per decade over the past half century. The first disturbance event was probably most intense given that most canopy trees established at that time and displayed high initial growth rates. The timing of the second disturbance event coincided with the documented selective logging. The last three disturbances, having lower tree growth responses and a clumped spatial distribution of gap creation, were probably the result of recurring typhoons. The first two disturbances led to tree regeneration and secondary succession, represented mainly by long-lived deciduous trees in the forest. The subsequent disturbances facilitated the stand development process, creating a complex three-dimensional structure from a pre-existing single-age cohort. This study suggests that EBLFs affected by large disturbances can recover in a few decades and the frequent gap disturbances probably facilitate its process in the early successional stages.

**Keywords** Dendroecology · Growth release · Disturbance history · Typhoon

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## Introduction

Disturbance plays an important role in determining the structure and functioning of ecosystems (Pickett and White 1985), and is also important in maintaining species diversity (Denslow et al. 1998). In forests, many tree species rely on gaps created by disturbances to reach the canopy from the understory, with different species requiring different gap attributes (size, longevity, frequency of occurrence) (Canham 1988, 1989). Disturbances with different intensities and frequencies at varying spatial scales can promote trees coexistence (Sousa 1984). Therefore, if we want to understand current species composition and forest stand structure, it is necessary to reconstruct historic disturbance regimes.

A method using dendrochronological data to derive past disturbance regimes has been widely applied in temperate forests to study successional dynamics and disturbance histories (Lorimer 1980; Lorimer and Frelich 1989; Abrams et al. 1995; Nowacki and Abrams 1997; Splechtna et al. 2005). With dendroecological techniques being increasingly applied to tropical tree species, the past disturbance regimes of tropical forests have been satisfactorily revealed (Worbes et al. 2003; Baker et al. 2005). However, there are few studies using dendroecological analyses to derive historical disturbances in subtropical forests (Grau et al. 2003).

Evergreen broadleaved forest (EBLF) is a major forest type in subtropical regions (Wu 1980; Kira 1991). It is the zonal vegetation in eastern China (Song and Cheng 2007). There are many types of natural disturbances in EBLF. Some of them are intense large-scale disturbances, which destroy large swaths of forests, such as landslides, catastrophic droughts, fires, and insect attacks (Li et al. 1997; Enoki 2003; Peng et al. 2003; Zhang et al. 2006). There are also less severe disturbances that facilitate fine-scale gap dynamics, such as typhoons, lightning strikes, heavy snowfalls, and individual tree senescence (Bao et al. 2001; Miura et al. 2001; Zhang et al. 2003, 2006). Typhoons are the most common natural disturbance in EBLFs that are located near the coast or on islands (Mabry et al. 1998; Miura et al. 2001; Fujita et al. 2003; Yang et al. 2006). They directly affect the forest canopy structure by creating different size gaps, thus providing chances for shade-intolerant species to regenerate and recruit upwards in the canopy (Yamamoto 1997; Miura et al. 2001). EBLF researchers have examined short-term dynamics caused by natural disturbances, most of them spanning less than 10 years (Bao et al. 2001; Miura et al. 2001; Zhang et al. 2006, but see Fujita et al. 2003). There are no reports covering longer time scales.

EBLF in eastern China has been heavily affected by human activities historically, and now it suffers from rapid economic development. There are four main types of anthropogenic disturbance: burning for agricultural conversion, human wars, logging for timber, and selective logging for firewood (Song and Cheng 2007). The last major anthropogenic disturbance occurred around 1960, in which numerous large trees were cut for fuelwood to make steel. These EBLFs are now second-growth forests. Due to intense anthropogenic disturbances, large areas of EBLFs in eastern China have already disappeared and the remnant forests are now highly fragmented (Wang et al. 2005; Song and Cheng 2007). However, the long-term influence of anthropogenic disturbances on EBLFs dynamics is poorly understood.

In this study, we reconstruct historical disturbances in an EBLF in eastern China, which was dominated by *S. superba* and *C. carlesii* based on an analysis of dendrochronological data of overstory trees. The objective of this article is to reveal the relationships between the disturbance histories, species composition, and stand structure of this forest. To meet this objective, these underlying questions are posed: first, how many disturbances occurred in this forest and what spatiotemporal pattern did they form; second, how did these disturbances affect the species composition and forest stand structure?

## Methods

### Study area

The study site is located in Tiantong National Forest Park(TNFP) (29°48′N, 121°47′E), Zhejiang Province, Eastern China, several kilometers inland from the East China Sea. Taibai Mountain is the highest peak, at 653 m above sea level and most other elevations are in the range of 100–300 m. The climate of this region is subtropical monsoon with mean annual temperature and precipitation of 16.2°C and 1375 mm, respectively. Parent materials are

Mesozoic sediments and acidic intrusive rocks, including quartzite and granite. The surface soil texture is mainly medium-heavy loam with a pH range of 4.4 to 5.1. Although most of the vegetation is thought to be secondary growth, the study site around the Buddhist Temple is likely a climax community. Here, the canopy is dominated by *Castanopsis fargesii*, *C. carlesii*, and *S. superba* (Song and Wang 1995; Yan et al. 2006; Huang et al. 2007).

Five 20 m × 20 m plots were established at 260 m above sea level on a 25–30° slope within TNFP in October 2003. The main composition of the forest was evergreen broad-leaved species of *Fagaceae*, *Camellia*, and *Symplocaceae* and the dominant species were *S. superba*, *C. fargesii*, and *Lithocarpus glaber* (Yang et al. 2005).

## Material and tree-ring measurements

In October 2003, we applied four types of logging disturbances on the forest to study recovery processes and mechanisms (Table 1) (Da and Song 2008). The cross-sectional wood discs of samplings and seedlings were obtained at the base of trees and the cross-sectional wood discs of mature individuals were obtained at a height of 0.3 m aboveground. After air-drying, the discs were sanded with 150 to 600 grit sandpaper (some up to grit 1500). For each disc, tree rings were measured along 2–4 radii to the nearest 0.001 mm using the WinDendro tree-ring image analysis software (Version 2003a, Regent Instruments [Sainte-Foy, Quebec, Canada]). Multiple radii from a tree were cross dated using the real-time cross-dating features of WinDendro, which could greatly facilitated the detection of false rings and missing rings. The radii values were averaged for each tree.

To reconstruct the historic disturbances, we used the tree-ring data of all trees taller than 8 m in plot I, plot II, and plotIII, except for three individuals of *C. carlesii* and one individual of *S. superba* that were shorter than the 8 m threshold (Table 2). Piths were missing in four individual discs. For these discs, the number of the missing tree-rings was estimated by using the average diameter growth rate of other individuals having a pith. As such, the residual chronologies of the four individuals without pith were also used in dendroecological analysis.

**Table 1** To simulate logging disturbances in the study area, four different manipulations were carried out in an EBLF dominated by *Schima superba* and *Castanopsis carlesii* in Tiantong forest National Forest Park, Ningbo, China

| | manipulations |
|---|---|
| PlotI | Harvested trees in the canopy that were taller than 8.0 m |
| PlotII | Harvested all plants aboveground, leaving the soil and litter |
| PlotIII | Harvested all plants aboveground, removing the topsoil (depth 0-10 cm) and litter |
| PlotIV | Harvested all trees under the canopy that were shorter than 8.0 m) |
| PlotV | The control, without any manipulation |

## Growth-release pattern analysis

When disturbances occur in mature forests, trees respond with increased radial growth due to higher light levels, more growing space and reduced competition (Canham 1988, 1989). In order to derive information about a disturbance event, we used the percent growth change (%GC) technique to evaluate radial growth changes. This method has been successfully used in temperate and tropical forests (Abrams et al. 1995; Nowacki and Abrams 1997; Baker et al. 2005; Splechtna et al. 2005). Radial-growth averaging is considered to be a valid technique for deriving past canopy disturbances and an effective alternative to detrending age-size relationships in tree-ring data (Lorimer and Frelich 1989; Nowacki and Abrams 1997). The first step of implementing this method is to determine the length of time to average radial growth rates. Lorimer and Frelich (1989) used a period of 15 years for radial-growth averaging to identify the growth releases expressed by shade-tolerant understory trees during canopy accession. A 10-year span was considered to be a reasonable criterion, since it tends to average out short-term growth responses related to climate while capturing intermediate-length increases in growth commonly associated with canopy disturbance (Nowacki and Abrams 1997; Baker et al. 2005; Brienen and Zuidema 2006). Alternatively, Payette et al. (1990) used a time span of 4–5 years. For our research, we selected a 5-year time span for radial-growth averaging to capture the high frequency typhoons and de-trend the 1–3 years fast-slow

**Table 2** Species used in the dendroecological analysis

| Species | Family | Life form | Age (means and range) | Number of samples |
|---|---|---|---|---|
| *Schima superba* | Theaceae | Evergreen tree | 56 (26–78) | 55 (1)[a] |
| *Castanopsis carlesii* | Fagaceae | Evergreen tree | 41 (20–56) | 22 (3) |
| *Lithocarpus glaber* | Fagaceae | Evergreen tree | 52 (32–58) | 5 |
| *Cyclobalanopsis myrsinaefolia* | Fagaceae | Evergreen tree | 51 (28–70) | 3 |
| *Castanopsis fargesii* | Fagaceae | Evergreen tree | 52 | 1 |
| *Cyclobalanopsis glauca* | Fagaceae | Evergreen tree | 39 | 1 |
| *Castanopsis sclerophylla* | Fagaceae | Evergreen tree | 43 | 1 |
| *Castanea seguinii* | Fagaceae | Deciduous tree | 52 | 1 |
| *Sassafras tzumu* | Lauraceae | Deciduous tree | 11 | 1 |
| *Alniphyllum fortunei* | Styracaceae | Deciduous tree | 45 | 1 |

All trees were in the forest canopy and taller than 8.0 m, except one individual of *Schima superba* and three individuals of *Castanopsis carlesii*

[a] Number in parentheses means the number of individuals without pith in cross-sectional wood disc

diameter growing rhythm exhibited in some evergreen tree species (Chen et al. 1998).

The second step of this method is to determinate the minimum %GC threshold to identify a canopy disturbance. It has been documented that radial-growth pulses in closed-canopy forests are largely dependent on gap formation and that canopy disturbances often have less influence on overstory trees than those in the understory (Nowacki and Abrams 1997; Splechtna et al. 2005). Trees also tend to respond more conservatively to canopy perturbations if it immediately follows another disturbance (Cao and Ohkubo 1999). Nowacki and Abrams (1997) considered radial-growth increases of 25% as a minimum threshold for canopy disturbance recognition for oak forests. Brienen and Zuidema (2006) regarded a growth increase of >100% as a growth release in a Bolivian rain forest. Baker et al. (2005) defined a >100% growth increase lasting 10 years as a “major release” and >50% growth increase lasting 10 years as a “moderate release” in a seasonal tropical forest. Considering the high frequency of typhoons in this region, radial-growth responses to continuous disturbances may be subtle or reduced. Therefore, we selected a growth increase of more than 50% to represent a minor release, and a growth increase of more than 100% as a major release.

Percentage growth change (%GC) was calculated in yearly increments across individual tree-ring chronologies using the formula of Nowacki and Abrams (1997):

$$\%\mathrm{GC}_i = [(M_2 - M_1)/M_1] \times 100$$

where $\%\mathrm{GC}_i$ is percentage of growth change for year $i$, $M_1$ is the mean annual diameter growth of the preceding 5-year period (including the year of change), and $M_2$ is the mean annual diameter growth of the subsequent 5-year period. Hence, for the percentage growth change in the year 1970, the $M_1$ would be the mean over the period 1966–1970 and the mean for $M_2$ would be calculated over the years 1971–1975. Since each %GC value represents a 10-year span of ring-width data, empty cells relative to source tree-ring chronologies inherently occur at both ends and the historical disturbances can only be reconstructed before 1998.

## Establishment pattern analysis

Canopy disturbances that form gaps often induce pulses of tree regeneration. Therefore, tree establishment patterns could be used to identify disturbance events. As a supplement to growth-release pattern analysis, periods of tree establishment were tracked by species. Trees established in large gaps under high light conditions often have fast initial growth rates (IGR) (Nowacki and Abrams 1997). IGR was inferred from the mean annual diameter increment of the five earliest rings in the disc (Baker et al. 2005). Here, we used a growth index to evaluate the early growing conditions of those trees used in the dendroecological analysis. It was defined as the ratio of those trees' IGR to the average IGR of the saplings younger than 20 year old, which established under more-or-less canopy conditions. A ratio >1.0 means a tree probably established in a small gap, whereas a ratio >1.5 means a tree probably established in a large gap. The early growing conditions were evaluated for trees with sufficient data: *C. carlesii*, *S. superba*, *L. glaber*, *Cyclobalanopsis myrsinaefolia* and *C. fargesii*. Individuals without piths were not used in this analysis.

We used both the distribution of growth-release pattern and establishment pattern to infer the number of historical disturbances and identify the exact periods when the disturbances occurred. We then coupled these results with tree mapping to portrayed tempo-spatial disturbance patterns (Payette et al. 1990). The spatial distribution of growth-release and establishment events was determined by using Ripley's *L*-function in SpPack (Perry 2004) (For more details, see Supplementary material).

## Results

### Growth-release pattern

The first growth release of *S. superba* occurred in 1939, and growth releases occurred in every decade until 1998 (Fig. 1b). There were five large peaks in growth release in every decade between 1940 and 1990, and in each peak, the percentage of tree showing release was more than 20%. The first peak occurred around 1950 with five trees releasing (25%) and two trees having major releases. The second peak occurred around 1960 with 11 trees releasing (20%) and three trees having major releases. The third peak occurred around 1970 with 17 trees releasing (30%) and 10 trees having major releases. The fourth peak occurred around 1980 with 25 trees releasing (45%) and 16 trees having major releases. The last peak occurred in the late 1980s with 19 trees releasing (30%) and seven trees having major releases.

The first growth release of *C. carlesii* occurred in 1960. Two large peaks in growth release occurred in the 1960s and 1980s. The peak in the 1960s could be divided into two small peaks and more than 50% trees released ($N = 6$) with two of them having major releases. The total number of releases was smaller in the second peak ($N = 5$, only 25%), but 75% of them had major releases (Fig. 1c). In total, the growth release pattern for the two co-dominated species had five peaks in growth release, the same as the pattern of *S. superba* (Fig. 1a).

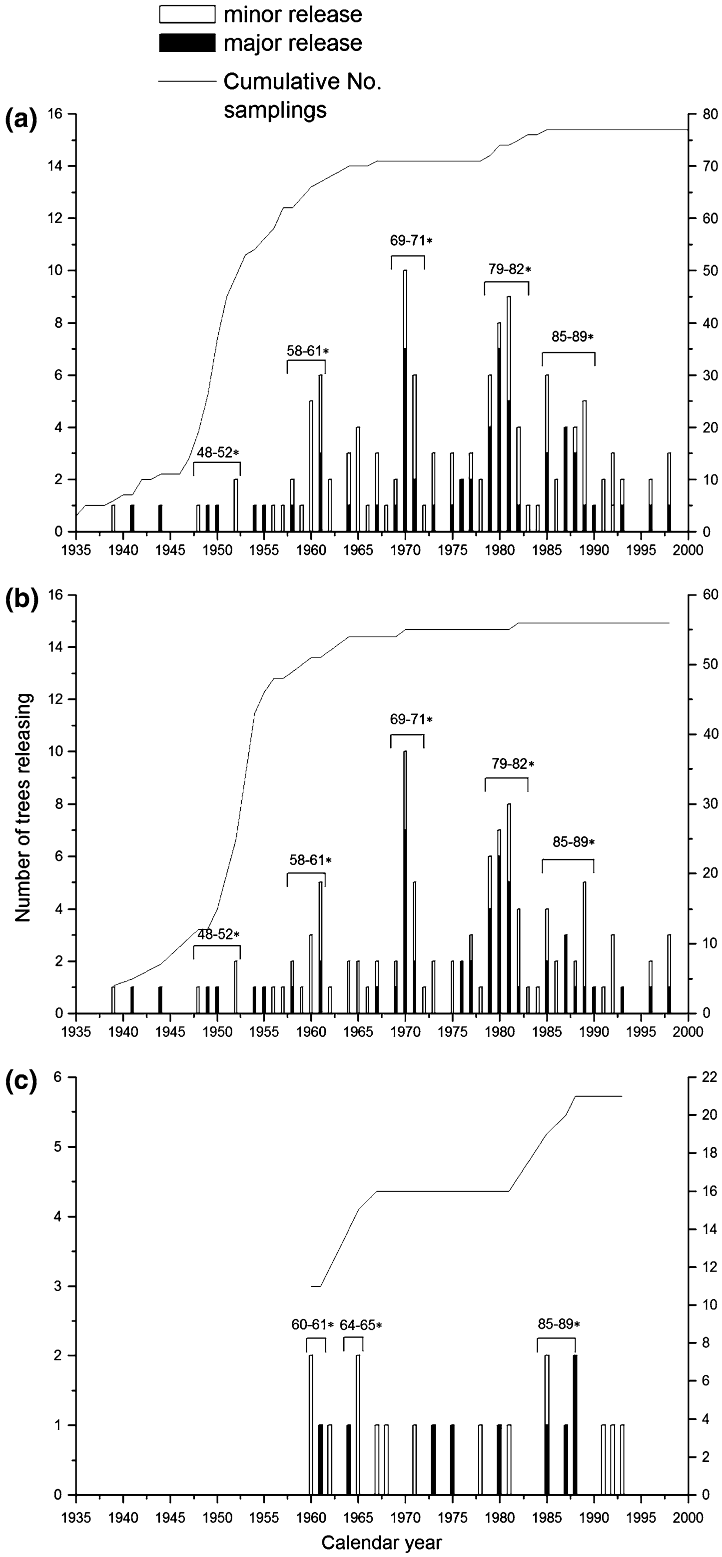
Most of the growth releases of other species occurred between 1955 and 1980. There were also two peaks around 1960 and 1980 (Fig. 2). *Castanea seguinii* and *Alniphyllum fortunei*, two highly shade-intolerant deciduous species, had a growth release in either peaks. This implies that the disturbance was severe enough to make a high-light environment fostering the growth of these two light-demanding species.

### Establishment pattern

Tree establishment of *S. superba* shows a brief recruitment peak around 1950. Sixty percent of *S. superba* established during this period (Fig. 3a). *C. carlesii* showed two recruitment peaks in 1945–1965 and the 1980s; more than 70% of them established in the first peak (Fig. 3b). All trees of *S. superba* and *C. carlesii* established in the late 1940s, 1950s, and early 1960s, and co-dominated the forest. Meanwhile, more than 70% of other species established in this period (Fig. 3c). Clearly, there was strong tree establishment in the middle of last century whereby both shade-tolerant, late-succession species and shade-intolerant, pioneer species such as *C. seguinii* and *A. fortunei* regenerated. This indicates that there was an intense disturbance creating a high-light environment for recruitment of shade-intolerant pioneer species.

The initial growth rate index of most trees was larger than 1.0, suggesting those trees grew at a faster rate after establishment than those established under the canopy. Twenty-three trees (43%) of *S. superba* were larger than 1.5 and most of them established in the first two growth-release peaks around 1950 and 1960 (Fig. 4a). *C. carlesii* had a similar pattern to *S. superba* (Fig. 4b), and the index of trees established around 1980 is significantly smaller than for trees established around 1950 and 1960 ($P < 0.05$). All individuals of other evergreen tree species had an

**Fig. 1** Growth-release pattern for both *Schima superba* and *Castanopsis carlesii* (**a**); growth-release pattern for *Schima superba* (**b**); growth-release pattern for *Castanopsis carlesii* (**c**). The line represented the sample size over time. Stars represent periods when the percentage of trees released more than 20%, which were regarded as disturbances



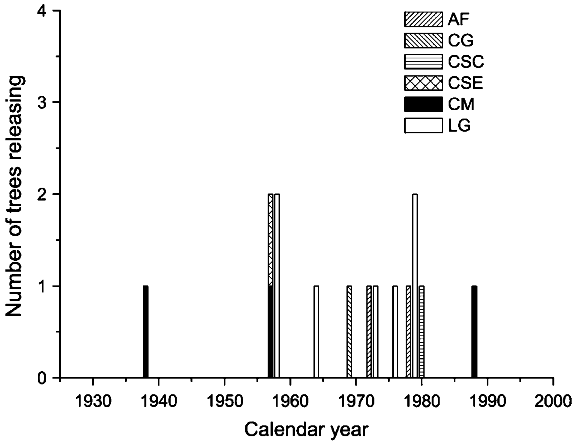


**Fig. 2** Growth-release patterns for other tree species. Species abbreviations are: AF, *Alniphyllum fortunei*; CG, *Cyclobalanopsis glauca*; CSC, *Castanopsis sclerophylla*; CSE, *Castanea seguinii*; CM, *Cyclobalanopsis myrsinaefolia*; LG, *Lithocarpus glaber*

index larger than 1.0 and only three of them were smaller than 1.5 (Fig. 4c). All the results suggest that the disturbances that occurred around 1950 and 1960 were more severe than subsequent disturbances.

## Spatial distribution of growth-release and establishment

Pulses of tree establishment corresponded with tree-ring growth releases on all plots (Fig. 5). Spatially, these events were randomly dispersed (Figs. S1–S3), but the mean $L(r)$ value of the last two peaks was larger than the mean value of the first two peaks at 5 and 10 m distance class in three plots (Table S1). This indicated that over time the spatial distribution tended toward clumping at 5–10 m distance class. There were a few individuals having a growth-release or establishment in both two proximate peaks, and the clumps of release and establishment events in a plot during two proximate peaks usually exhibited a mosaic pattern. It is clear in plotII that the clumps were composed of different individuals for the last two peaks and the clumps in the fourth peak were close to those in the last peak.

Compared to the crown projection map, the locations at the clumps of the release and establishment events in the last two peaks had denser crown projections (Fig. 6). For example, the dense crown

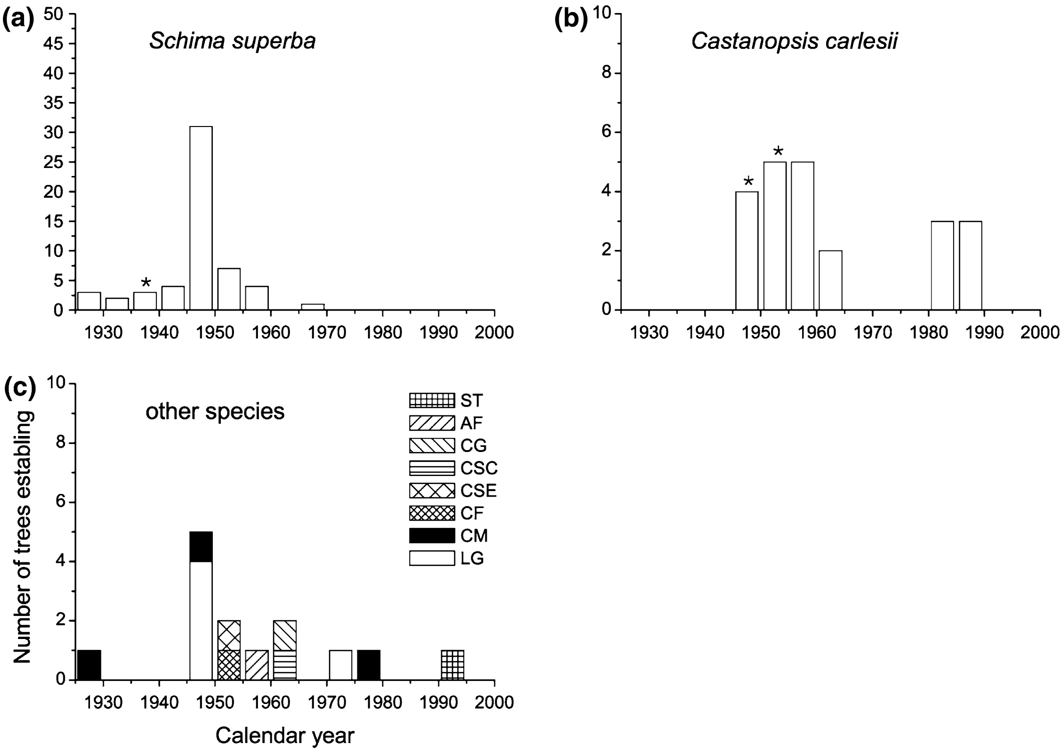


**Fig. 3** Establishment patterns for *Schima superba* (**a**), *Castanopsis carlesii* (**b**), and other trees (**c**). Species abbreviations are as in Fig. 2, besides ST, *Sassafras tzumu*; CF, *Castanopsis fargesii*. *Stars* represent individuals without pith that were included

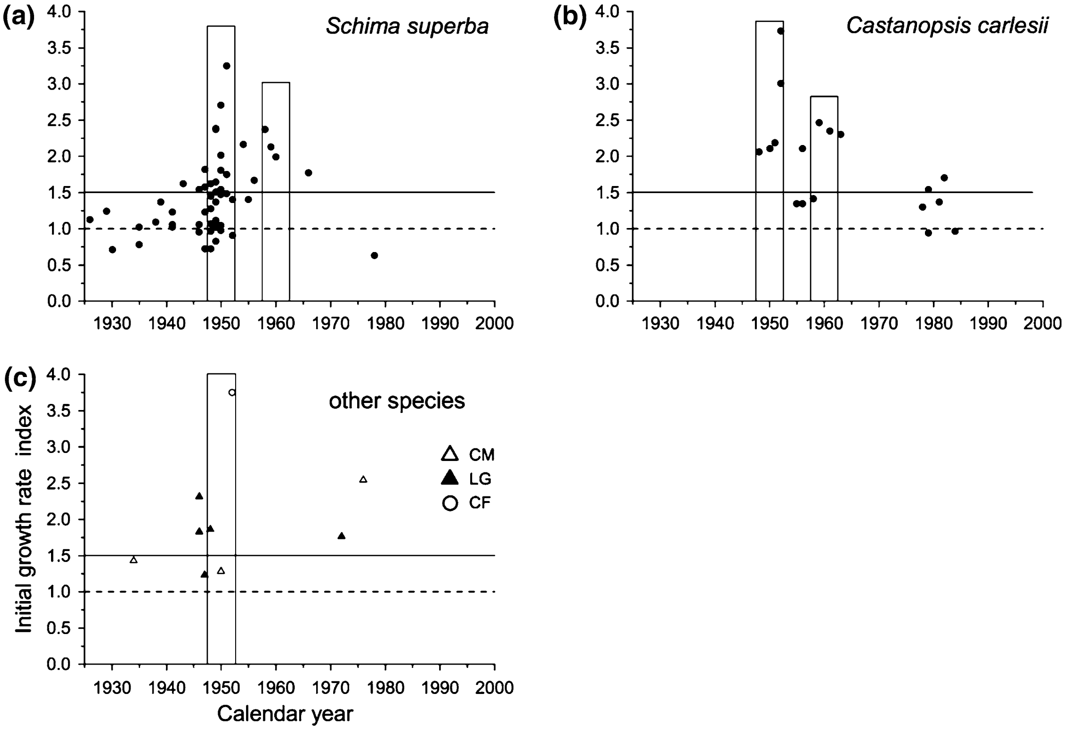


**Fig. 4** Distribution of initial growth rate index for *Schima superba* (**a**), *Castanopsis carlesii* (**b**), and other trees (**c**). The trees established in the first two growth-release peaks around 1950 and 1960, are contained in rectangles. Species abbreviations are as in Figs. 2 and 3. The individuals without pith could not be used to calculate the initial growth rate, so the number of *Schima superba* and *Castanopsis carlesii* is 54 and 19, respectively. Sufficient data were not available for the other study species

projections at the top right corner in plot I correspond to the clump composed of five major release events in the fourth peaks (Fig. 5d), and the dense crown projections in the middle of plotII correspond to the clump in the last peak (Fig. 5e). This indicates that the clump of the release and establishment events may represent a gap, and the trees under the gap or beside the gap competed intensely, thus forming a dense closed canopy. On the other hand, gaps may be maintained or extended by repeated disturbances causing larger open spaces, such as that in plot III, which may be the result of the last two disturbances.

## Discussion

### Historic disturbance regime: a combination of anthropogenic and natural disturbances

According to the growth-release and tree establishment patterns, there were five distinct disturbances that occurred in the second half of the last century. The first disturbance occurred around 1950 and had by far the largest effect on this forest. Subsequent disturbances occurred on average every 10 years. The second disturbance was the only one that had historical documentation. In order to generate fuel for the local steel industry, many large trees were logged between 1958 and 1960. The first disturbance had an even greater effect on increasing the initial growth rate of established trees than the second disturbance (Fig. 4), so we considered the first disturbance to be the most intensive one. We did not know exactly what kind of disturbance it was, but there was a civil war occurring at that time that might have impacted the stand.

Compared to the first two disturbances, there were fewer canopy trees established in the last three disturbances. The initial growth rates of trees were smaller during these disturbances, indicating that these disturbances created rather small gaps. The study region is close to the coastline of the East China

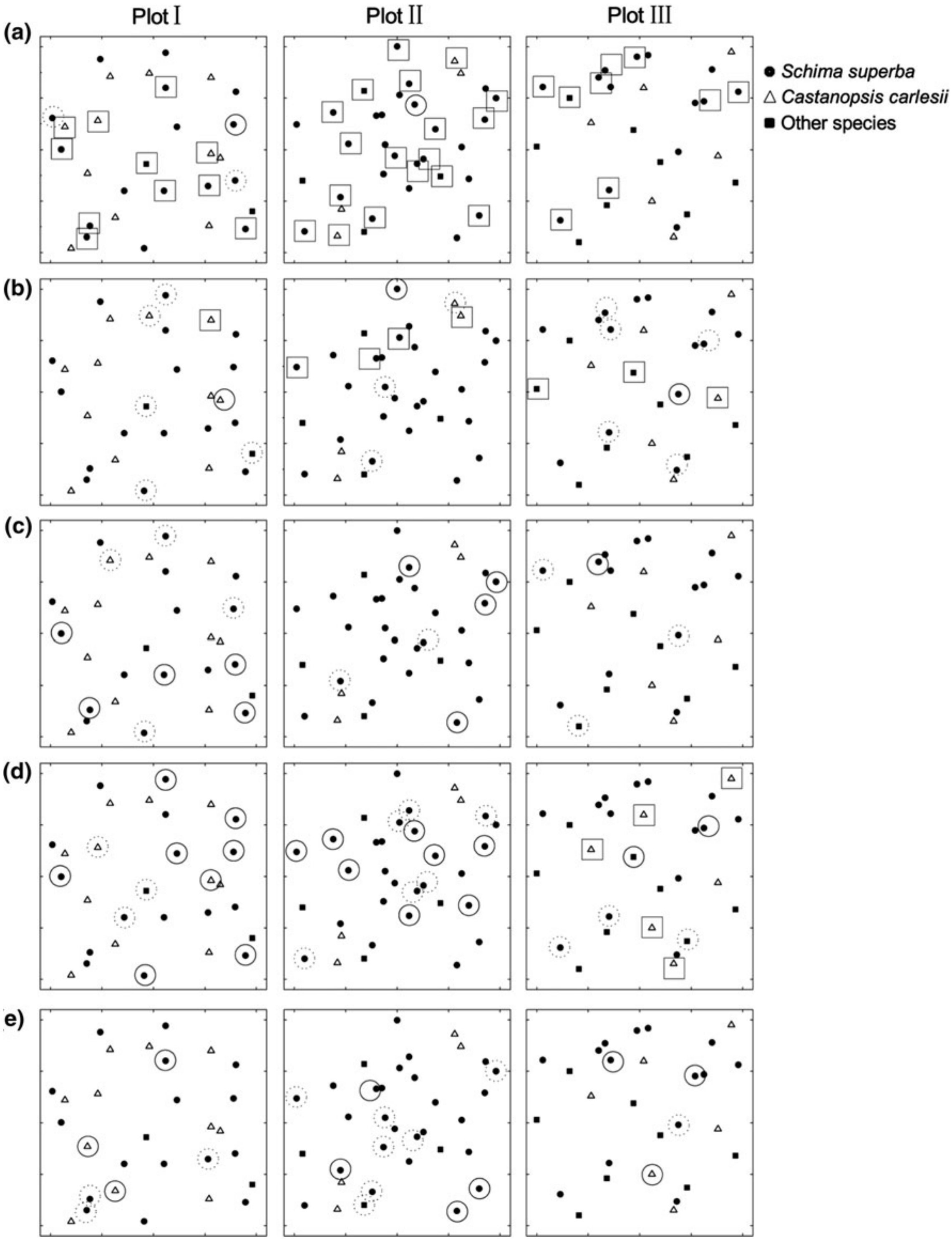


**Fig. 5** Spatial distribution of the growth-releases and establishments during the five peaks in growth-release: the period around 1950 (**a**), 1960 (**b**), 1970 (**c**), 1980 (**d**) and the period in the late 1980s (**e**), respectively. *Circles with solid lines* represent a major release; *circles with dotted lines* represent a minor release; rectangles represent an establishment. Other species are the same as in Fig. 3

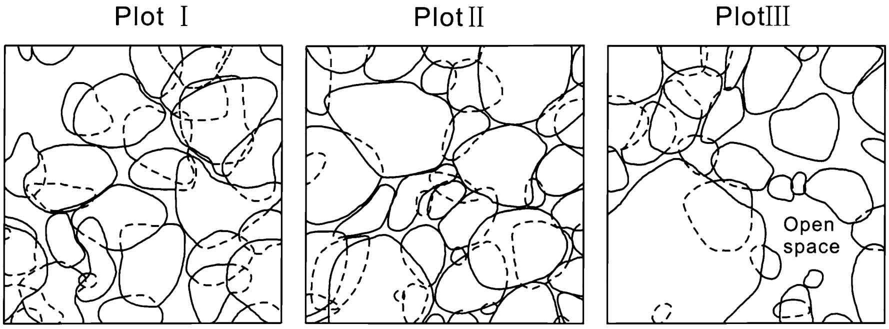


**Fig. 6** The crown projection maps for all trees taller than 8.0 m in three plots. The *dotted lines* mean those crowns were shaded by other trees. At the right side of plot III, there was an open space with a sparse canopy

Sea, and typhoons pass through or near this region each year (See Fig. S4). Typhoons became the major disturbance factor after 1970 when this forest was protected from human activity (Jiang et al. 2007). Two powerful typhoons in 2005 created many canopy gaps, although most were smaller than 100 $m^2$ in size (Yang et al. 2006). This is similar to the size of clumps of release and establishment events found in our study. In the tropical forest of Taiwan, the average size of gaps caused by typhoon is 33 $m^2$ (Mabry et al. 1998). In the mature evergreen broad-leaved forest of the South Island of Tsushima, the mean gap size is 77–138 $m^2$ due to different methods in measurement (Yamamoto 1997; Fujita et al. 2003; Miura et al. 2001).

We used the percentage of individuals having two release events in the last three disturbances over 30 years to calculate the annual canopy gap formation rate. The result is 0.550%, which is more than the rate of 0.278% that has been reported in this region (Jiang et al. 2007), but falls in the range of the rate of 0.5–2.0% in the South Island of Tsushima (Miura et al. 2001; Fujita et al. 2003). Nevertheless, the clumps of release and establishment events in different disturbances border on each other, giving indirect evidence that a single canopy gap formation could promote another disturbance because of the increase in risk of death of gap-bordering trees, especially in forests with frequent typhoons. This gap formation process may cause gap expansion via the connection of neighboring gaps (Fujita et al. 2003), as the formation of large open space in plot III. Meanwhile, when the new neighboring gap occurred, the older gap closed because of lateral extension or regeneration (Miura et al. 2001), causing a dense canopy.

### Forest composition and structure responded to disturbances

The first two intense disturbances made a high-light environment for tree regeneration and recruitment; indeed most of the individuals in the present-day canopy established after these disturbances, forming a forest that is dominated by a single cohort. In this cohort, there were not only the shade-tolerant species *C. carlesii* and *C. fargesii* considered to be the climax species in this region (Song and Wang 1995; Da et al. 2004), but also the light-demanding deciduous trees *C. seguinii* and *A. fortunei* that are considered pioneer species in this subtropical forest. The population structure of the two pioneer species had a uni-modal distribution (Yang et al. 2005), which suggested that there was a rare intense disturbance causing long-lived shade-intolerant pioneer species to remain in the canopy without prompting seedling recruitment. This pattern was also reported in a season tropical forest (Baker et al. 2005) and an old mature evergreen broadleaved forest (Miura et al. 2001; Fujita et al. 2003).

*Schima superba* is a common species in early successional forest as it has wind-dispersed seeds and prefers to recruit in sunny locations (Song and Wang 1995; Da et al. 2004). The intense disturbance created a high-light environment that favored *S. superba*. Moreover, as a “nutrient conservative” species with low leaf nutrient and high nutrient resorption efficiency (Yan et al. 2006; Huang et al. 2007), *S. superba* could persist in soils depleted by soil erosion which often accompanies intense disturbance (Pickett and White 1985). With a strong ability to re-sprout, *S. superba* could persist long-term on site even after intense disturbances (Song and Cheng

2007; Wang et al. 2007). All these advantages would explain *S. superba*'s dominance in this forest. Although *C. carlesii* is a shade-tolerant species, it too has a strong ability to re-sprout (Wang et al. 2007) and a higher growth rate than *S. superba* (Song et al. 2008), allowing it to quickly recapture growing space after intense disturbances. It was similar to *Castanopsis cuspidata* var. *sieboidii*, one of the major canopy trees in evergreen broadleaved forests (EBLF) in Japan, which tended to show higher recruitment because it sprouts profusely from stems damaged during disturbance (Miura et al. 2001; Miura and Yamamoto 2003a, b).

The last three gap-disturbance events did not significantly change the composition in the canopy, but they created canopy recruitment opportunities for some subordinate trees established during prior disturbances. According to the tree-ring data, most growth releases occurred in the last three gap-disturbance events, especially those with major growth releases (Fig. 1). Previous research indicated that the time under suppression for *S. superba*, *C. carlesii*, and *L. glaber* was no more than 20 years (Song et al. 2008). Our research suggests that a gap disturbance occurred in each decade in this forest stand. Therefore, the frequent gap disturbances were helpful to shift the growth rates from slow (suppressed) to fast (released), and played an important role in canopy accession of evergreen broadleaved species. The importance of gaps for canopy recruitment has been underscored in temperate forests (Nowacki and Abrams 1997; Cao and Ohkubo 1999) and tropical forests (Baker and Bunyavejchewin 2006).

The regeneration and recruitment of light-demanding deciduous species, such as *Choerospondias axiliaris*, *A. fortunei*, and *Sassafras tzumu*, are closely associated with gaps (Song and Cheng 2007). The seedlings of *S. superba*, which prefer gaps, were clumped in the open space that was inferred to have been caused by the last two disturbances. It was similar with *Schima wallichii* whose juveniles were concentrated on the forest floor just adjacent to canopy gaps in an evergreen forest on Amami Oshima Island, in southwestern Japan (Enoki 2003). Although *C. carlesii* can germinate under closed canopy and gaps, its saplings were concentrated in the large open gaps in plot III, which indicates that the gaps promoted the recruitment of the mid-sized individuals of *C. carlesii*. In a few decades, this process led the population structure to shift from a simple single cohort to a reverse J-shaped distribution (e.g., *C. carlesii*) or to a sporadic multi-peaked distribution (e.g., *S. superba*) (Yang et al. 2005). Therefore, the gap-disturbances not only provided opportunities for coexistence of evergreen shade-tolerant species and deciduous shade-intolerant species in this EBLF forest, but also increased the heterogeneity and complexity of the overall structure of the forest.

However, the frequency of canopy disturbances caused by recurrent typhoons may have prevented succession from proceeding to later stages (Miura et al. 2001). This may explain why *S. superba* is distributed widely in the study region and why it can coexist with species in climax communities (Song and Wang 1995).

## Assessing the method: using dendroecological analysis to reconstruct historical disturbances in EBLFs

In our research, a total of five canopy disturbances were identified from tree-ring data, yet only two of them resulted in distinct pulses of tree establishment. Baker et al. (2005) reconstructed the historical disturbances using four methods: stand structure, estimated age distribution, establishment pattern and dendroecological analysis. By comparing the results of these four methods, it was shown that tree-ring data provides the most accurate means of identifying and dating past disturbances, which corresponds with our findings. Because the responses of woody plants to disturbances differ (Canham 1989), it is important to choose suitable species that are responsive to canopy disturbances. Our results indicate that tree-ring series of *S. superba* identified five disturbances, more than three of *C. carlesii*, and that more individuals of *S. superba* had growth releases in a given disturbance, especially where gaps occurred. It suggests that species like *S. superba*, whose growth rate is sensitive to the change in light environment, are superior in recording disturbance events.

In addition, the tree-ring series can provide information about the initial growth rate after germination. By comparing the growth rate of trees established in openings versus those under canopies, we can ascertain the post-disturbance light environment and in turn the degree or the severity of the canopy disturbance. Combining this with the dendroecological analysis and plotting them onto a spatial distribution map, the regimes of historical disturbances could be more accurately described.

Researches on disturbances in EBLFs were more often focused on coastline regions or islands with frequent wind disturbances (Yamamoto 1997; Miura et al. 2001; Yang et al. 2006; Jiang et al. 2007). Little is known about EBLFs on the mainland where fewer disturbances are observed, such as the EBLFs in western China. Since *Castanopsis*, *Lithocarpus*, *Cyclobalanopsis*, *Schima*, *Machilus* and other common genera in EBLF have clear tree rings (Cheng et al. 1992), we suggest that dendroecological analysis can be performed in these forests as well, providing insights into their disturbances dynamics.

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