

Effects of natural and artificial disturbance on landscape and forest structure in Tiantong National Forest Park, East China

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Abstract This paper aims to understand the ecological effects of disturbance on broadleaved evergreen forest in East China. We used a manipulative field experiment approximating the common natural and artificial disturbance types in this area to investigate the community physiognomy, floristic composition, and 5-year recovery dynamics of the post-disturbance forest community. The results indicated that the landscape and forest structure have degraded into shrub communities, structure-damaged evergreen broadleaved communities, and so on. The post-disturbance communities presented different means of plant recruitment and vegetation recovery patterns at an early successional stage. The recovery of disturbed forests primarily depended on external seed sources and re-

sprouting from stumps, rather than on soil seed banks, as few buried seeds were found. Re-sprouting thus appears to be key in allowing rapid vegetation recovery in evergreen broadleaved forest. Disturbances seem to be one of the most important factors that can contribute to regional species coexistence across temporal and spatial scales in evergreen broadleaved forests.

Keywords Evergreen broadleaved forest · Long-term field experiment · Community physiognomy · Community dynamics

Introduction

The effects of disturbance on forest ecosystem degradation have been widely recognized (Ren et al. 2007). Disturbances, whether natural or man-made, play a crucial role in determining forest structure and dynamics (Sousa 1984; Pickett and White 1985; McNab et al. 2004). Following natural disturbances, there is often an increase in heterogeneity at both spatial and temporal scales, which range in scale from frequent small-scale canopy gaps created by the deaths of individual trees (Busing and White 1997; Parish and Antos 2004; Bebi et al. 2009) to rare catastrophic disturbances, such as hurricanes and fires, that may destroy extensive areas of forest (Abrams et al. 1995; Peterson 2000; Ulanova 2000; Baker et al. 2005; D'Amato and Orwig 2008). The rates of change in vegetation types can also be directly or indirectly influenced by human activities, with humans acting as disturbance agents in their interactions with the physical environment and successional processes (Kennedy and Spies 2004).

Evergreen broadleaved forest (EBLF) is an important forest formation unique to the warm-temperate/subtropical

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region (Wu 1980; Kira 1991). It is dominated by evergreen trees of the genera *Cyclobalanopsis* (*Quercus*), *Castanopsis* and *Lithocarpus* and associated evergreen species, such as *Cinnamomum*, *Ilex*, *Symplocos*, and *Camellia* (Song et al. 2005). In the case of EBLF in Eastern China, long-term, frequent human activities have had substantial effects on the forest ecosystem, as have natural events such as typhoons. As a result, mature climax EBLF now exists in very few areas, with the majority being remnant secondary forests, secondary shrub communities, and grass and bush communities (Song and Chen 2007). Many Chinese ecologists have studied the causes of degradation of EBLF under different disturbance levels (Song and Wang 1995; Li and Song 2003; Da et al. 2004; Yang et al. 2006; Song and Chen 2007; Wang et al. 2007a, b). However, these studies primarily document the vegetation types and floristic composition of the current degraded communities and deduce the possible vegetation dynamics after historical disturbance events. Little is actually known about the long-term dynamics of post-disturbance vegetation (Da and Song 2008).

Recently, community ecologists have been placing emphasis on experimental approaches to vegetation ecology (Cook et al. 2005; Da and Song 2008). This approach may reveal important patterns and processes that have not been detected by other methods, and may further supplement and perfect both current community theories and non-experimental empirical studies. Long-term experimental and observational studies, combined with comparative and theoretical work, provide a unique perspective on the organization of communities. These are now being used to detail long-term vegetation dynamics (Rees et al. 2001; McGarigal and Cushman 2002) and the regeneration processes after disturbance.

The specific objectives of this study were (1) to clarify the response process of community dynamics in evergreen broadleaved forest, (2) to understand the role of seed banks and re-sprouters to vegetation recovery after different disturbances, and (3) to discuss the important role of disturbance on regional species coexistence at multiple scales.

Materials and methods

Study site

The study site is located in Tiantong National Forest Park (29°53'N, 121°39'E), Zhejiang Province, East China, several kilometers inland from the East China Sea. Taibai Mountain is the highest peak, at 653 m above sea level; most other elevations are in the range of 100–300 m. The climate of this region is subtropical monsoon with a mean annual temperature and precipitation of 16.2°C and

1,374.7 mm, respectively. The substrate parent materials are Mesozoic sediments and acidic intrusive rocks, including quartzite and granite. The soil texture is mainly medium-heavy loam with a pH range of 4.4–5.1 (Song and Wang 1995). Although all of the vegetation is thought to be secondary, the forest around the Buddhist Temple is believed to be, at least in part, the mature forest approximating the climax community. The canopy is dominated by *Castanopsis fargesii* Franch., *Castanopsis carlesii* (Hemsl.) Hayata. and *Schima superba* Gardn. et Champ.

Disturbance history

Natural and artificial disturbances of varying magnitudes have occurred periodically in this area. Small-scale canopy gaps usually arise from the death of individual trees due to snags, typhoons, or selective logging (Jiang et al. 2007). Typhoons, a principal natural disturbance regime to forest ecosystems, frequently occur between July and October, resulting in powerful winds, high rainfall, and landslides. Human influences such as forest clearance, agriculture activities, and plantations are also considered an important factor shaping forest dynamics across a range of scales. In the 1950s, this area was subjected to selective logging of many adult trees (Song and Chen 2007).

Manipulative field experiment by simulated disturbances

Five 20 m × 20-m plots, at 260 m above sea level, with a 25°–30° slope, were established within Tiantong National Forest Park (TNFP) in October 2003. The main composition of the community was evergreen broad-leaved species of *Fagaceae*, *Camellia*, and *Symplocaceae*, and was dominated by *Schima superba*, *Castanopsis carlesii*, and *Lithocarpus glaber* (Thunb.) Nakai (Yang et al. 2006). Four plots were disturbed by four different treatments according to the common natural or artificial disturbance types of this area, and the remaining one was free of disturbances (Da and Song 2008; Table 1). All the manipulations were carried out simultaneously in October 2003 (Fig. 1). Plants were harvested by saw and ax, and each stump was left. The litter and topsoil (0–10 cm) in plot II and plot III were also artificially removed.

In post-disturbance plots, long-term monitoring investigations were carried out from 2004 to 2008. Within each subplot, the species, DBH (diameter at breast height), and height of trees $H \geq 1.5$ m tall were measured. In the stratum $H < 1.5$ m, tree species were recorded, and the height of tree seedlings and maximum height of shrubs and herbs were measured. The coverage of each species was estimated by Braun-Blanquet method (Song 2001).

Table 1 Description of different treatments and simulated disturbance types

Plot	Treatments	Simulation disturbance types
I	Logging trees that were taller than 8.0 m	Gap formation by selective logging or typhoon
II	Clear-cutting aboveground vegetation	Abandoned reclamation upland after repeated cutting
III	Plot II + removing litter and topsoil (0–10 cm)	Landslide or water erosion or mining
IV	Cutting all plants that were shorter than 8.0 m and leaving others	Standard forestry management practice
V	The control, without any manipulation	

Fig. 1 Post-disturbance state of five plots under different treatments

A 20×20 -m sized plot was established for studying the seed banks next to disturbed plots in October 2005. The plot was divided into 16 equal sections, from each of which a $50 \times 50 \times 10$ -cm sample of soil was randomly collected. The soil was washed through a 0.15-mm mesh sieve, and the seeds spread evenly on sterilized potting soil in a seed tray and placed in a laboratory at East China Normal University. The direct germination method of Thompson and Grime (1979) was used to assess germination. As seedlings emerged, they were identified, counted, and removed to facilitate tracking of newly germinating seedlings.

Data analysis

Species basal area (BA, cm^2) was calculated from the DBH of individual trees. In each plot, relative BA (RBA, %) of each species was used as an abundance measure of that species, and the dominant species were determined based on dominance analysis (Ohsawa 1984).

The similarity between seed banks and tree seedlings was analyzed by the Jaccard index and χ^2 coefficient (McKinney 2004).

Results

Changes in community structure and physiognomy

Overall, the floristic composition, dominant species, and community height of 5-year post-disturbance communities were considerably different from undisturbed communities (Table 2). The EBLF in these plots was degraded into secondary shrub community after severe disturbance. In plot I, there were 30 evergreen species and 13 deciduous species. Six evergreen species and three deciduous species (see in Table 2) were co-dominated, and their maximum height was 5–7 m, representing a mixed shrub community that was dominated by evergreen species. In plot II,

deciduous species *Litsea cubeba* (Lour.) Persoon (59.2%) and *Choerospondias axillaris* (Roxb.) Burt et Hill (12.9%) were co-dominated, and the total RBA was over 70.0%. This represents a deciduous shrub community with 3–5-m heights. Plot III was dominated by a mixed shrub community of deciduous species with 3–5-m heights. There were five dominant species (see in Table 2), and the total RBA of deciduous species *Litsea cubeba* and *Sassafras tzumu* (Hemsl.) Hemsl was higher than in the other three evergreen dominance species. Plot IV and plot V were covered by evergreen broadleaved forest dominated by *Schima superba* and *Castanopsis carlesii* with 18–20 m heights, but the former community structure had been destroyed.

Table 2 Floristic composition, dominant species, and community height among evergreen broadleaved forest in 5-year post-disturbance communities

Plot	I	II	III	IV	V
Number of evergreen species	30	18	13	17	28
Number of deciduous species	13	12	14	14	14
Community height (m)	5–7	3–5	3–5	18–20	18–20
	RBA (%)	RBA (%)	RBA (%)	RBA (%)	RBA (%)
Evergreen trees					
<i>Castanopsis carlesii</i>	42.5*	6.0	9.7*	12.8*	5.6
<i>Cinnamomum camphora</i>	7.3*	2.6	5.5*		
<i>Lithocarpus glaber</i>	3.4*	1.3	5.4*	5.3	8.9
<i>Myrica rubra</i>	1.9		2.9		
<i>Schima superba</i>		3.8	3.1	44.6*	66.6*
<i>Castanopsis fargesii</i>		1.2	3.5		
<i>Cyclobalanopsis myrsinaefolia</i>			1.3	2.8	
<i>Cyclobalanopsis sclerophylla</i>				1.8	1.5
Evergreen shrubs					
<i>Symplocos heishanensis</i>	4.8*			3.8	
<i>Symplocos sumuntia</i>	3.5*				
<i>Eurya nitida</i>	3.4*				
<i>Eurya muricata</i>	3.0				
<i>Camellia fraterna</i>	2.7				
Deciduous trees					
<i>Choerospondias axillaris</i>	5.0*	12.9*	5.1		
<i>Alniphyllum fortunei</i>	2.1	1.2			
<i>Sassafras tzumu</i>	1.4	6.9	15.9*		
<i>Liquidambar formosana</i>			2.0	3.8	4.5
<i>Pinus massoniana</i>				24.6*	
<i>Quercus fabri</i>					1.8
Deciduous shrubs					
<i>Litsea cubeba</i>	6.0*	59.2*	39.5*		
<i>Styrax confuses</i>	3.7*	1.2	1.2		
<i>Clerodendrum cyrtophyllum</i>			1.2		

Dominant species of each plot are indicated by asterisk. Species with small relative basal area (RBA < 1%) is omitted

Changes in community dynamics at the early recovery stage

The height class distribution of early recovery communities has changed significantly over the past 5 years (Fig. 2). In plot I, 5 years later, the number of stems over 3.0 m increased from 32 to 187, and evergreen species accounted for 68.1% of the tree species composition. These were primarily remnants of saplings and shrub species. The maximum height of trees in the plot reached 6.7 m. In plot II, 1 year after disturbance, only four stems were found that exceeded 1.5 m in height, with 1,016 stems below 1.5 m. The majority of these were shade-intolerant pioneer species, which had profuse rapid growth and were best adapted

to exploit the high-light environment in gaps. Five years later, 70.0% of the stems were taller than 1.5 m, and the maximum had reached 6.5 m. The dominant species were deciduous trees *Choerospondias axillaris* and *Litsea cubeba*. The re-sprouts of evergreen trees accounted for 20.1%. It thus appears that re-sprouting has played an important role in the recovery of evergreen trees in this area. In plot III, the 1-year recovery pattern was similar to that of plot II, but the number of stems was reduced. Three years later, none of the stems were taller than 3.0 m. Five years later, only 5.4% of these stems were taller than 3.0 m. In plot IV, growth was slow; there was only one stem taller than 3.0 m after 5 years apart from the remnant trees over 8.0 m. The regeneration partly relied on the

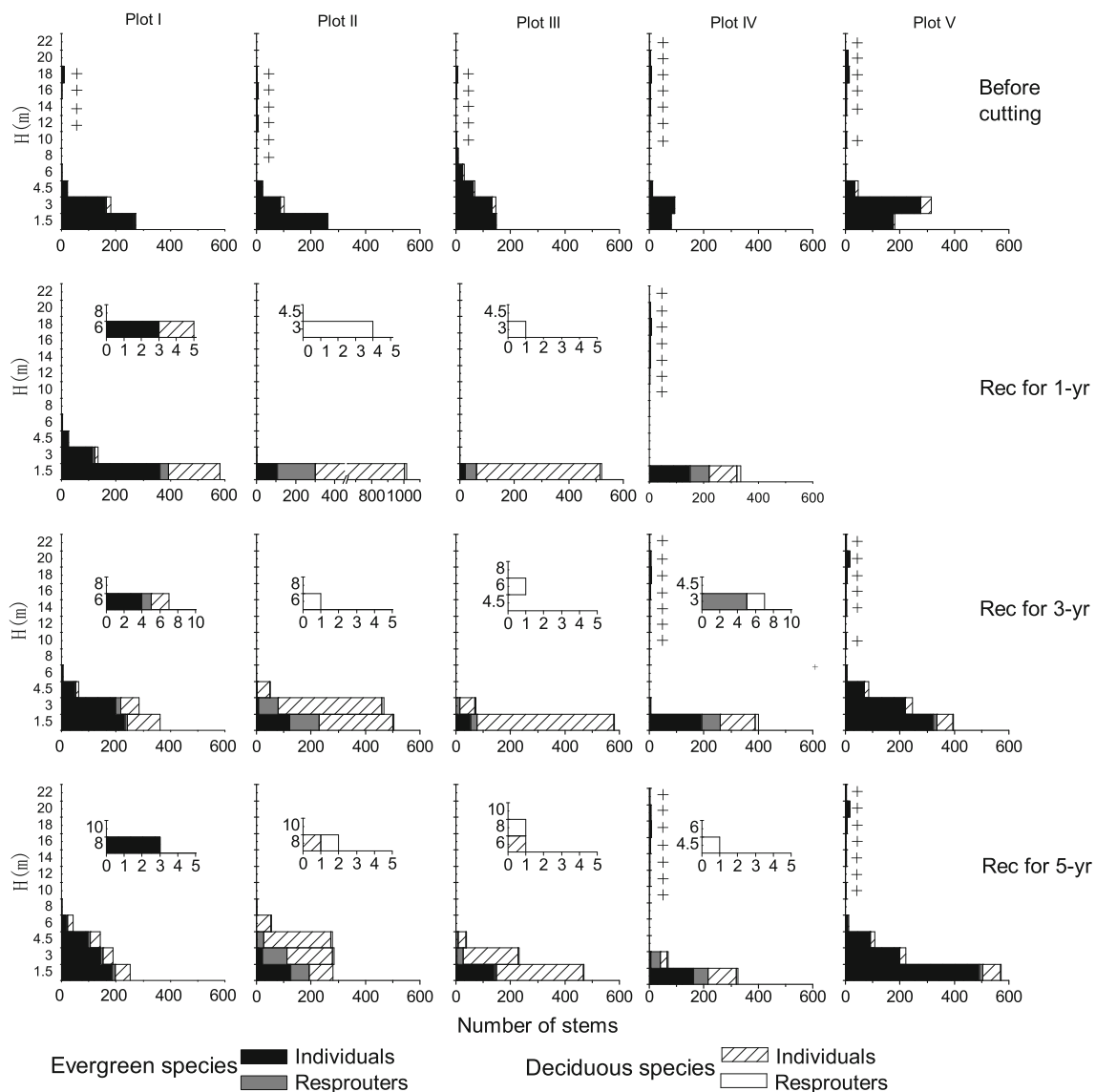


Fig. 2 Height class distribution of post-disturbance communities at the early stages. ‘+’ indicates the existence of higher trees in the class with low densities. The small figure in upper right indicates the

existence of lower trees in the class with low densities. ‘Rec for 1-yr’ means recovery for 1 year

Table 3 Relationship between the seed bank and composition of vegetation after different disturbances

Index	Plot I	Plot II	Plot III	Plot IV
Jaccard index	0.200	0.179	0.162	0.184
χ^2 coefficient	0.0185	1.2850	0.7810	0.0022

$$df = 1, \chi^2_{0.01} = 6.635, \chi^2_{0.05} = 3.841$$

re-sprouting of evergreen or deciduous trees, accounting for 24.6%. In plot V, the plants over 1.5 m did not change in any obvious manner, although there was a relative increase in the late-successional species.

Similarities between seed banks and the seedlings compositions of the first year recovery

There were 995 seeds in the seed bank, and the seed abundance was 248.75 m^{-2} . In the seed bank, more than 60% of the species present were herbs (Song et al. 2010). Evergreen tree species accounted for only 1.46%, and these were predominantly the four species *Schima superba*, *Lithocarpus glabra*, *Lithocarpus harlandii* (Hance ex Walpers) Rehder, and *Castanopsis carlesii*. The similarity between the seed banks and seedlings after the first year of recovery in each plot, as indicated by the Jaccard similarity index, were initially low (Table 3). The Jaccard similarity indexes for the seed banks and 1-year seedlings in plots I, II, III, and IV were 0.200, 0.179, 0.162, and 0.184, respectively. This indicates that the seed banks contributed relatively little to the first-year vegetation recovery.

Discussion

Vegetation recovery dynamics and its factors

This simulated experimental study indicates that early vegetation recovery is characterized by different patterns. In plot I, the remnant juvenile *Schima superba* and *Castanopsis carlesii*, and shrubs *Symplocos sumuntia* Buch.-Ham were free to grow, and they rapidly dominated the upper layers of community (Table 2; Fig. 2). Because of the change of light availability and microenvironment after canopy gap formation, the understory vegetation was released from shade and broke through the regeneration bottleneck (Denslow et al. 1998; Miura et al. 2001). Moreover, previous studies using dendroecological methods have also suggested that the medium-diameter *Castanopsis carlesii* and *Schima superba* are released and grow rapidly in canopy gaps induced by frequent typhoons in this area (Song et al. 2007, 2008). Hence, advanced regeneration takes place when suppressed individuals are released after disturbance.

In contrast, when understory vegetation ($H < 8 \text{ m}$) was cleared out, as in plot IV, the post-disturbance vegetation regenerated and developed slowly, and the height-class changed negligibly at the early stage (Fig. 2). Two years later, the majority of ferns and herbs, including *Dryopteris* sp. and *Woodwardia japonica* (Lf) Sm, had re-established in moist and dark conditions (Da and Song 2008). Acting as an ecological filter, the forest floor stratum with a higher coverage of ferns and herbs impeded seed germination and seedling emergence, primarily through reduction in light levels (George and Bazzaz 1999). This represented one of the first potential barriers to tree regeneration so that vegetation recovery was impeded after removal of understory vegetation.

In plot II, where topsoil and litter had been retained, the abundance and height of deciduous pioneer species increased rapidly during the early stage (Fig. 2). The dynamics of plot II represented the normal pattern of secondary succession dominated by *Litsea cubeba* and *Cherospondas axiliaris* (Table 2). In plot III, where the topsoil had been removed, the vertical structure of the community changed slowly compared to plot II (Fig. 2). Although a few plants can be collectively distributed on 'fertile islands,' many plants were unable to effectively colonize and grow normally under nutrient-impooverished soil conditions after disturbance (Uhl et al. 1981; Velázquez and GmeóZ-Sal 2008). Thus, the progress of secondary succession may be severely delayed by soil disturbances such as those in plot III.

Moore's (1980) hypothesis has suggested that vegetation and seed bank composition should be similar in frequently disturbed communities and should be dominated by early successional annuals with persistent seed banks (Kalamees and Zobel 2002; Roovers et al. 2006). Our results indicated that the contribution of the seed bank to vegetation re-establishment was little, as seen from the Jaccard similarity index (Table 2). This conclusion was supported by the low seed densities observed in mature forests in this area, which were 249 m^{-2} in this study and $73\text{--}141 \text{ m}^{-2}$ in a *Castanopsis fargesii* forest (Mo 1995). This seed density is even lower than that of the evergreen broad-leaved forest in Japan, which was estimated at $427\text{--}1,190 \text{ m}^{-2}$ in the *Castanopsis cuspidata* (Thunb.) Schott. forest of Hiroshima and at $218\text{--}940 \text{ m}^{-2}$ in the *Fagus crenata* Blume forest of southwestern Japan (Nakagoshi 1984, 1985). Other supporting evidence also comes from the observation that seeds of late-successional species did not germinate easily (Mo 1995), and there were plenty of light-demanding trees that colonized in disturbed habitats from external seed sources (Dalling and Hubbell 1998). Evergreen broad-leaved trees generally have a lower fecundity rate in a mature forest and many *Fagaceae* seeds, which are characterized by high starch content, are prone to predation or

rotting, or germinating immediately during the current year's seed input (Zhang et al. 1999). Furthermore, there were many individuals of light-demanding species *Mallostus apelt* (Lour.) Muell.-Arg., *Dalbergia hupeana* Hance, *Choerospondias axillaries*, *Albizia kalkora* (Roxb.) Prain, *Machilus thunbergii* Sieb. et Zucc., and *Cinnamomum camphora* (L.) Presl that occurred in plot II and plot III (Song et al. 2010).

Re-sprouting as a means of long-term in situ persistence is common and might be the ancestral state in woody angiosperms (Wells 1969). In this study, many trees, both evergreen species and deciduous species, could re-sprout from the remnant stumps in each plot and accounted for a significant proportion of vegetation recovery in plot II and plot IV (20.1 and 24.6%, respectively Fig. 2). Other studies have also reported that many evergreen broadleaved trees, including *Schima superba*, *Lithocarpus glaber*, and *Castanopsis sclerophylla* (Lindl.) Schot in this area, were highly tolerant of cutting because of re-sprouting, long-time persistence of the stumps, effective allocation of

surplus energy to sprouts, and biomass recovery in secondary succession (Peter 2000; Bond and Midgley 2001; Wang et al. 2004; Yan et al. 2005; Shang et al. 2008). Therefore, re-sprouting of evergreen trees could compensate for the low seedling recruitment and repeated cutting in this area (Song and Wang 1995).

Landscape diversity and regional species coexistence at multi-scales

Three shrub communities with different physiognomies (PI, PII, and PIII) and one structure-damaged evergreen broadleaved community (PIV) were formed after different simulated disturbances in plots. These four communities represent different stages of disturbed communities. Frequent human activities and typhoons have seriously disturbed the evergreen broadleaved forest, resulting in many patches of plantation, degraded forest, and even bare soil (Song and Chen 2007). The plantations are mainly located on lowland areas and often consist of monocultures or

Table 4 Community type and floristic composition of evergreen broad-leaved forest and degraded communities (Song and Wang 1995; Wang et al. 2007a, b)

Physiognomy type	Community type	Family	Genera	Species
Mature climax evergreen broad-leaved forest	<i>Castanopsis fargesii</i> + <i>Schima superba</i> association <i>Cyclobalanopsis nubii</i> + <i>Lithocarpus henryi</i> carpeto <i>Lithocarpus henryi</i> association	78	162	262
Mature evergreen broad-leaved forest (near climax)	<i>Schima. Superba</i> + <i>Castanopsis sclerophylla</i> community <i>Machilus thunbergii</i> Community; <i>Cinnamomum camphora</i> community	43	71	100
Deciduous broad-leaved forest	<i>Ulmus parvifolia</i> + <i>Celtis tetrandra</i> ssp. <i>sinensis</i> community <i>Liquidambar formosana</i> + <i>Platycarya strobilacea</i> community	33	51	61
Coniferous and broad-leaved mixed forest	<i>Pinus massoniana</i> + <i>Schima superba</i> community <i>Pinus massoniana</i> + <i>Castanopsis Sclerophylla</i> community <i>Pinus massoniana</i> + <i>Liquidambar Formosana</i> + <i>Cinanamomum camphora</i> community <i>Pinus massoniana</i> + <i>Celtis tetrandra</i> ssp. <i>sinensis</i> + <i>Broussonetia papyrifera</i> community	40	66	84
Coniferous forest	<i>Pinus massoniana-Loropetalum chinense</i> community <i>Pinus massoniana-lindera reflexa</i> community <i>Pinus massoniana-Schima superba-Dicranopteris pedata</i> community <i>Pinus massoniana-Liquidambar formosana</i> + <i>Loropetalum chinense</i> community <i>Pinus massoniana-Dalbergia hupeana</i> community <i>Pinus massoniana-Cinnamomum camphora</i> + <i>Melia zaedarach</i> community <i>Cunninghamia lanceolata-Schima superba</i> community <i>Cunninghamia lanceolata</i> community	59	105	149
Secondary shrub community	<i>Quercus fabri</i> + <i>Loropetalum chinense</i> community <i>Quercus fabri</i> + <i>Symplocos setchuensis</i> community <i>Schima superba</i> + <i>Cylobalanopsis glauca</i> community <i>Platycarya strobilacea</i> + <i>Indocalamus tessellates</i> community <i>Dalebergia hupeana</i> + <i>Mallotus tenuifolius</i> community	59	107	146

artificial communities such as *Phylostachys pubescens* Mazel ex H. de Lehaie communities, tea gardens, orchards, and rice paddies for wood production and economic development (Song and Wang 1995). The remnant mature forests are often degraded into immature EBLF, deciduous broad-leaved forest, coniferous and broad-leaved mixed forest, and coniferous forest after low-intensity disturbance, and secondary shrub communities arise from repeated cutting for firewood or soil erosion (Table 4, Wang et al. 2007a, b). This landscape was similar to satoyama in Japan (Kobori and Primack 2003).

Mixed landscapes provide varied habitat types and often contribute to species diversity across temporal and spatial scales (Olff and Ritchie 2002; Kobori and Primack 2003). The total number of spermatophytes encountered in this area was 968 species belonging to 506 genera and 149 families (Song and Wang 1995). As is shown in Table 4, 262 species are coexisting in mature climax forests, while the number of species in degraded communities is no more than 160. However, the pioneer deciduous trees *Broussonetia papyrifera* (L.) Vent. *Celtis tetrandra* ssp. *sinensis* Y.C. Tang and *Melia azedarach* L. (Table 4), and a majority of annual and extensive-distribution herbs, such as *Erigeron annuus* (L.) Pers., *Xanthium sibiricum* Patr. ex Widdeer, and *Digitaria sanguinalis* (L.) Scop., were not found in mature climax forest (Wang et al. 2007a, b). Thus, diversity landscapes provided more opportunity for species coexistence at a large spatial scale.

At temporal scales, the secondary successional series of communities consists of bare land, shrub communities of *Lithocarpus glaber*-*Loropetalum chinense* community, *Pinus massoniana* community, *Pinus massoniana*-*Schima superba* communities, *Schima superba* communities, and *Castanopsis fargesii* communities (Song and Wang 1995; Ding 1999). At the early stage of succession, *Pinus massoniana* Lamb, *Schima superba*, and *Castanopsis sclerophylla* were predominant in the canopy layer. *Castanopsis fargesii* and *Lithocarpus glaber*, instead of *Pinus massoniana* and *Castanopsis sclerophylla*, gradually dominated in the canopy layer as succession progressed. In the shrub layer, *Albizia kalkora*, *Callicarpa bodinieri* Levl., *Lespedeza formosa* (Vog.) Koehne, *Quercus fabri*, *Castanea seguinii* Dode, *Dalbergia hancei* Benth., and *Euscaphis japonica* (Thunb.) Kanitz decreased (Song and Wang 1995). Conversely, the number of species including *Loropetalum chinense* (R. Br.) Oliv., *Symplocos sumuntia*, *Rhododendron simsii* Planch., *Vaccinium sbracteatum* Thunb., *Viburnum dilatatum* Thunb., *Camellia fraterna* Hance, *Rhododendron ovatum* Planch., and *Symplocos stellaris* Brand increased, and they eventually became dominant species in the shrub layer (Li 1995). Thus, communities at different successional stages could support a greater diversity of species at temporal scale.

Conclusion

Disturbance played an important role in determining the landscape and forest structure of evergreen broadleaved forest in East China. The floristic composition and community physiognomy were altered by different disturbances. The post-disturbance communities showed different means of plant recruitment and vegetation recovery patterns at the early stages of succession. Re-sprouting appeared to be a key trait and may speed up vegetation recovery, while the seed bank appeared to play a much smaller role. Hence, disturbances seem to be one of the most important factors that can contribute to species diversity across temporal and spatial scales in evergreen broadleaved forests. Furthermore, long-term experimental and observational studies are needed to further understand the vegetation dynamics of evergreen broadleaved forest.

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References

- Abrams MD, Orwig DA, Demeo TE (1995) Dendroecological analysis of successional dynamics for a presettlement-origin white-pine-mixed-oak forest in the southern Appalachians, USA. *J Ecol* 83:123–133
- Baker PJ, Bunyavejchewin S, Olive CD, Ashton PS (2005) Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecol Monogr* 75:317–343
- Bebi P, Kulakowski D, Rixen C (2009) Snow avalanche disturbances in forest ecosystems-State of research and implication for management. *For Ecol Manag* 257:1883–1892
- Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol Evol* 16(1):45–51
- Busing RT, White PS (1997) Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* 78:562–568
- Cook WM, Yao J, Foster BL, Holt RD, Patrick BL (2005) Secondary succession in an experimentally fragmented landscape: community patterns across space and time. *Ecol* 86(5):1267–1279
- D'Amato AW, Orwig DA (2008) Stand and landscape-level disturbance dynamics in old-growth forests in western Massachusetts. *Ecol Monogr* 78(4):507–522
- Da LJ, Song K (2008) Experimental ecology research on destroyed evergreen broad-leaved forests in TNFP, Zhejiang (I): ecological restoration experiments and long-term ecological study. *J East China Normal Univ (Nat Sci)* (4):1–11 (in Chinese with English abstract)

- Da LJ, Yang YC, Song YC (2004) Population structure and regeneration types of dominant species in an evergreen broad-leaved forest in Tiantong National Forest Park, Zhejiang province, Eastern China. *Acta Phytocol Sin* 28(3):376–384 (in Chinese with English abstract)
- Dalling JW, Hubbell SP (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *J Ecol* 86:674–689
- Denslow JS, Ellison AM, Sanford RE (1998) Tree-fall gap size effects on above- and below-ground process in a tropical wet forest. *J Ecol* 86:597–609
- Ding SY (1999) Comparative ecology of successive seral of evergreen broadleaved forest. Henan University Press, Kaifeng (in Chinese with English abstract)
- George LO, Bazzaz FA (1999) The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80(3):833–845
- Jiang LC, Liu LZ, Wang XH (2007) Forming characteristics of gap in an evergreen broad-leaved forest in Tiantong National Forest Park, Zhejiang Province, Eastern China. *J East China Normal Univ (Nat Sci)* 6:88–96 (in Chinese with English abstract)
- Kalamees R, Zobel M (2002) The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology* 83(4):1017–1025
- Kennedy RSH, Spies TA (2004) Forest cover changes in the Oregon Coast Range from 1939 to 1993. *For Ecol Manag* 200:129–147
- Kira T (1991) Forest ecosystem of East and South-East Asia in a global perspective. *Ecol Res* 6:185–200
- Kobori H, Primack RB (2003) Participatory conservation approaches for satoyama, the traditional forest and agricultural landscape of Japan. *Ambio* 32(4):307–311
- Li XD (1995) Succession of evergreen broadleaved forest. In: Song YC, Wang XR (eds) *Vegetation and flora of Tiantong National Forest Park, Zhejiang Province China*. Shanghai Science and Technology Literature Press, Shanghai, pp 114–142 (in Chinese with English Abstract)
- Li JX, Song YC (2003) Landscape classification and mapping with remotely sensed data for Tiantong National Forest Park in Zhejiang Province. *Chin J Ecol* 22(4):102–106 (in Chinese with English abstract)
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol Appl* 12(2):335–345
- McKinney ML (2004) Measuring floristic homogenization by non-native plants in North America. *Global Ecol Biogeogr* 13:47–53
- McNab WH, Greenberg CH, Berg EC (2004) Landscape distribution and characteristics of large hurricane-related canopy gaps in a southern Appalachian watershed. *For Ecol Manag* 196:435–447
- Miura M, Manabe T, Nishimura N, Yamamoto SI (2001) Forest canopy and community dynamics in a temperate old-growth evergreen broad-leaved forest, south-western Japan: a 7-year study of a 4-ha plot. *J Ecol* 89:841–849
- Mo JP (1995) Seed bank and seedlings bank of evergreen broadleaved forest. In: Song YC, Wang XR (eds) *Vegetation and flora of Tiantong National Forest Park, Zhejiang Province China*. Shanghai Science and Technology Literature Press, Shanghai, pp 79–92 (in Chinese with English Abstract)
- Moore PD (1980) Soil seed banks. *Nature* 284:123–124
- Nakagoshi N (1984) Buried viable seed population in forest communities on the Hiba Mountains, South-western Japan. *J Sci Hiroshima Univ B Div* 2(19):1–56
- Nakagoshi N (1985) Buried viable seed seeds in temperate forests. In: White J (ed) *The population structure of vegetation*. Junk, Dordrecht, pp 551–570
- Ohsawa M (1984) Differentiation of vegetation zones and species strategies in the subalpine region Mt. Fuji. *Vegetatio* 57:15–52
- Olliff H, Ritchie ME (2002) Fragmented nature: consequences for biodiversity. *Landscape Urban Plan* 58:83–92
- Parish R, Antos JA (2004) Structure and dynamics of an ancient montane forest in coastal British Columbia. *Oecologia* 141:562–576
- Peter JB (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* 89(2):409–416
- Peterson CJ (2000) Catastrophic wind damage to North American forests and the potential impact of climate change. *Sci Total Environ* 262:287–311
- Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press Inc., San Diego pp 472
- Rees M, Condit R, Crawley M, Pacala S, Tilman D (2001) Long-term studies of vegetation dynamics. *Science* 293:650–655
- Ren H, Shen WJ, Lu HF, Wen XY, Jiang SG (2007) Degraded ecosystems in China: status, causes and restoration efforts. *Landscape Ecol Eng* 3:1–13
- Roovers P, Bossuyt B, Igodt B, Hermy (2006) May seed banks contribute to vegetation restoration on paths in temperate deciduous forest? *Plant Ecol* 187(1): 25–38
- Shang KK, Chen B, Da LJ (2008) Experimental ecology research on destroyed evergreen broad-leaved forests in TNFP, Zhejiang (III): analysis of the adaptive strategy of common species in evergreen broad-leaved forest from caloric values. *J East China Normal Univ (Nat Sci)* 4:25–30 (in Chinese with English abstract)
- Song YC (eds) (2001) *Vegetation ecology*. East China Normal University Press, Shanghai pp 559 (in Chinese)
- Song YC, Chen XY (eds) (2007) Degradation mechanism and ecological restoration of evergreen broad-leaved forest ecosystem in East China. Science Press, Beijing, pp 339–354 (in Chinese)
- Song YC, Wang XR (eds) (1995) *Vegetation and flora of Tiantong National Forest Park, Zhejiang Province China*. Shanghai Science and Technology Literature Press, Shanghai (in Chinese with English Abstract)
- Song YC, Chen XY, Wang XH (2005) Studies on evergreen broad-leaved forests of China: a retrospect and prospect. *J East China Normal Univ (Nat Sci)* (1):1–8 (in Chinese with English abstract)
- Song K, Da LJ, Yang TH, Yang XF (2007) Age structure and growth characteristic of *Castanopsis fargesii* population. *Chin J Appl Ecol* 18(2):254–260 (in Chinese with English abstract)
- Song K, Yang XF, Kang MM, Da LJ (2008) Experimental ecology research on destroyed evergreen broad-leaved forests in TNFP, Zhejiang (II): the growth patterns of dominant evergreen trees determined by tree ring analysis. *J East China Normal Univ (Nat Sci)* 4:12–24 (in Chinese with English abstract)
- Song YB, Zhang QP, Da LJ (2010) Experimental ecology research on destroyed evergreen broad-leaved forests in TNFP, Zhejiang (IV): the contribution of seed bank to early restoration of destroyed evergreen broad-leaved forests. *J East China Normal Univ (Nat Sci)* 3:1–9, 56 (in Chinese with English abstract)
- Sousa WP (1984) The role of disturbance in natural communities. *Annu Rev Ecol Syst* 15:353–391
- Thompson K, Grime JP (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J Ecol* 67:893–921
- Uhl C, Clark K, Clark HMP (1981) Early plant succession after cutting and burning in the Upper Rio Negro Region of the Amazon Basin. *J Ecol* 69(2):631–649
- Ulanova NG (2000) The effects of windthrow on forest at different spatial scales: a review. *For Ecol Manag* 135:155–167
- Velázquez E, Gmez-Sal A (2008) Landslide early succession in a neotropical dry forest. *Plant Ecol* 199:295–308
- Wang XH, Yan X, Yan ER, Jin Y (2004) Primary study on sprout regeneration of several dominant species of evergreen broad-

- leaved forest after logging in Tiantong. J Wuhan Bot Res 22(1):52–57 (in Chinese with English abstract)
- Wang XH, Fang XF, Chen WJ, Yan ER (2007a) Characteristics and types of degraded evergreen broad-leaved forest in East China. In: Song YC, Chen XY (eds) Degradation mechanism and ecological restoration of evergreen broad-leaved forest ecosystem in East China. Science Press, Beijing, pp 39–88 (in Chinese with English abstract)
- Wang XH, Kent M, Fang XF (2007b) Evergreen broad-leaved forest in Eastern China: its ecology and conservation and the importance of resprouting in forest restoration. For Ecol Manag 245:76–87
- Wells PV (1969) The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23:264–267
- Wu ZY (ed) (1980) Vegetation of China. Science Press, Beijing (in Chinese)
- Yan ER, Wang XH, Shi JY, Wang XB, Wang LY (2005) A review on resprouting in woody plants. Chin J Appl Ecol 16(12): 2459–2464 (in Chinese with English abstract)
- Yang YC, Da LJ, Chen B (2006) Population structure and spatial patterns for the main tree species in *Castanopsis carlesii*-*Schima superba* community in Tiantong, Zhejiang Province, China. Acta Ecol Sin 26(9):2928–2938 (in Chinese with English abstract)
- Zhang DJ, Ye XY, You WH (1999) Evergreen broad-leaved forest floor in Tiantong, Zhejiang Province. Acta Phytoecol Sin 23(66):544–556 (in Chinese with English abstract)