

Evergreen broad-leaved forest in Eastern China: Its ecology and conservation and the importance of resprouting in forest restoration

Xi-Hua Wang^a, Martin Kent^{b,*}, Xiao-Feng Fang^a

^aDepartment of Environmental Science, East China Normal University, Shanghai 200062, China

^bSchool of Geography, University of Plymouth, Drake Circus, Plymouth, Devon PL4 8AA, UK

Received 26 May 2006; received in revised form 13 March 2007; accepted 24 March 2007

Abstract

Biogeographical and ecological research on the evergreen broad-leaved forests (EBLF) of the Far East, which have been reduced to remnant fragments over the historical period has, until now, been very limited. To inform forest conservation and management, this paper describes research into major plant community types and underlying environmental gradients of degraded EBLF in Eastern China and examines the importance of resprouting as a key mechanism in secondary succession following forest clearance. Species composition was described from 199 10 m × 10 m plots and analysed using two-way indicator species analysis and canonical correspondence analysis ordination. Some 22 degraded and mature forest community types were identified, while CCA indicated that a primary vegetation gradient was related to distance of sample plot from mature forest, which was closely linked to altitude and slope. The secondary gradient corresponded to successional stage and disturbance. The roles of resprouting and reseedling characteristics in forest regeneration were researched firstly by 10 m × 10 m plots from selected TWINSPAN groups and secondly by 20 m × 20 m plots in representative areas of forest at 1, 20, 43 and 60 years and in an area of mature forest.

The importance of resprouting in the regeneration of many EBLF tree and shrub species is demonstrated, a process linked to ideas of the persistence niche. Existing remnant forests should be conserved but forest restoration is also essential and will benefit from understanding of the importance of tree/shrub resprouting, as well as seedling recruitment in forest regeneration. Further work is required on seedbanks, germination success and both inter- and intra-specific competition within Chinese EBLF to assist with successful forest conservation and management.

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Keywords: Anthropogenic disturbance; Canonical correspondence analysis (CCA); Forest degradation; Forest management; Persistence niche; Succession; Two-way indicator species analysis (TWINSPAN)

1. Introduction

Evergreen broad-leaved forest (EBLF) is now recognised as an important global vegetation formation type that contributes to both the biodiversity and the sustainable development of the subtropical regions of China (Wu, 1980; Wang et al., 2005). The most comprehensive global overview of EBLF was completed by Ovington (1983) but unfortunately, as stated in his Preface, reference to the EBLF of China is conspicuously absent from that volume, partly because of the relatively limited amount of research into this vegetation type but also because such research results as existed were only reported in Chinese. For similar reasons, discussion of the forests is omitted in Archibold (1995), although they are mapped as EBLF in the

recent overview of world vegetation types by Box and Fujiwara (2005). While its biogeographical status in China still remains a matter of debate, unfortunately, the extent of the EBLF has decreased very significantly due to long-term anthropogenic disturbance, including deforestation, logging and fire, and much of the forest is now degraded to plantation, secondary forests, shrub and grassland communities.

1.1. The biogeographical status of EBLF

Song (1988, 1995) provides the most valuable review in English of both the position of the Chinese EBLF within the world vegetation formation types and the overall characteristics of the forest. In China, it occurs between 24 and 32°N and 99–123°E and formerly covered around 25% of the area of the country (Fig. 1). It lies within areas dominated by a sub-tropical monsoon climate, with mean annual temperatures between 15

* Corresponding author. Tel.: +44 1752 233061; fax: +44 1752 233054.

E-mail address: mkent@plymouth.ac.uk (M. Kent).

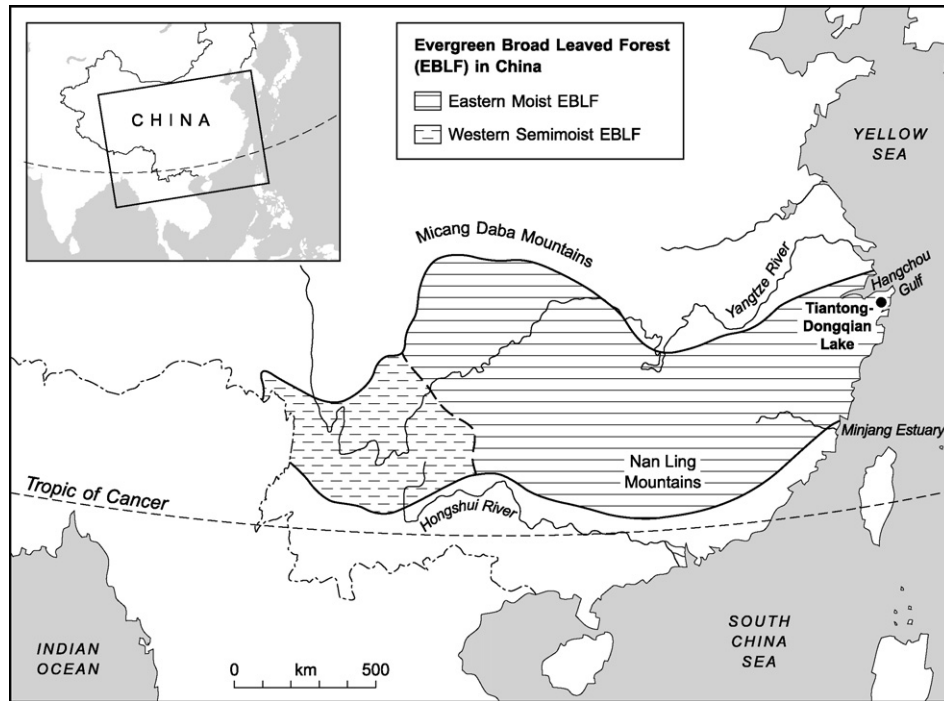


Fig. 1. The distribution of evergreen broad-leaved forest in China and the separation of forest into the Western semi-moist and Eastern moist forest types (after Song, 1988).

and 20 °C, a January minimum of 3–10 °C and a July maximum of 26–28 °C. Mean annual precipitation is between 900 and 2000 mm, with a summer maximum and a frost period of 64–100 days (Song, 1988). The forests occupy mountainous and hilly areas across the south and east of China and smaller local altitudinal floristic sub-gradients occur. The forests are extremely diverse, particularly in terms of tree and shrub species (phanerophytes 50–80% of species), ranging from over 100 vascular plant species/400 m² in the south, to 30–45 species in the north of its distribution (Hu, 1979; Song, 1988). The dominant species of the EBLF come from only a few genera, together with some ancient coniferous species, many of which have ‘broad leaves’ (Table 1). A high number of Chinese subtropical and East Asian endemic species also occur (Table 1). The herb layer of the forests is usually sparse, although the fern flora is significant. Both evergreen and deciduous lianas are important components, along with various epiphytes and bryophytes.

The EBLF zone within China is divided into two sub-regions: (a) the moist EBLF in Eastern China, influenced by the Pacific Ocean monsoon and (b) the semi-moist EBLF in the west, determined more by the Indian Ocean monsoon (Fig. 1). The annual rainfall is 1000–2000 mm in the moist east and 900–1200 mm in the semi-moist west. Detailed variations are explained in Song (1988, 1995). Ovington (1983) designated the EBLF type ‘temperate broad-leaved rain forest’ and placed it on a global scale with the ‘temperate broad-leaved sclerophyll forest’ and the ‘temperate evergreen seasonal forest’, jointly named ‘temperate broad-leaved evergreen forest’. However, Song (1995) maintains that the Chinese EBLF is distinctly different from both the true Mediterranean sclerophyllous

forests and those characteristic of the southern hemisphere, in Australia, New Zealand, Chile and South Africa. Following Klötzli (1988), he thus proposed that the Chinese EBLF should be seen as a separate global vegetation formation type and biome called the ‘monsoon sub-tropical evergreen broad-leaved forest’, characterised by a monsoon climate. However, this biome is not exclusive to the EBLF of China and similar forests to the eastern moist monsoon EBLF also occur in Japan, Korea and in the southeastern United States, in addition to the western semi-moist sub-tropical monsoon EBLF in China.

1.2. Degraded EBLF and resprouting mechanisms

The majority of the monsoon EBLF in China now exists as secondary degraded forest. The role of fire within the Chinese EBLF is thought to have been much less important in the past than in other evergreen broad-leaved forest areas such as the Mediterranean, Australia or South Africa. Rather than showing evidence of being fire-adapted, many tree species have physiognomic characteristics more similar to tropical forests, particular in their leaf structures (Song, 1988). Given the importance and dominance of anthropogenic disturbance and land use change in determining the composition of the degraded communities, research is required into their successional and regeneration dynamics.

The importance of resprouting of both trees and shrubs as a mechanism for species persistence and regrowth has not been given sufficient recognition generally and certainly in the case of the degraded communities of the EBLF. Resprouting allows species to persist in a site even after a wide range of disturbances over hundreds of years. Resprouting ability

Table 1
Dominant genera and endemic species of the EBLF in China (Song, 1988)

Dominant genera
<i>Beilschmidia</i>
<i>Camellia</i>
<i>Castanopsis</i>
<i>Cinnamomum</i>
<i>Cyclobalanopsis</i>
<i>Dryopteris</i>
<i>Eurya</i>
<i>Lindera</i>
<i>Lithocarpus</i>
<i>Machilus</i>
<i>Hicriopteris</i>
<i>Phoebe</i>
<i>Photinia</i>
<i>Prunus</i>
<i>Rhododendron</i>
<i>Schima</i>
<i>Woodwardia</i>
Ancient coniferous genera
<i>Catheyia</i>
<i>Cunninghamia</i>
<i>Fokienia</i>
<i>Pseudotsaxus</i>
<i>Taxus</i>
Sub-tropical endemic species
Chinese sub-tropical endemics
<i>Camellia fraterna</i>
<i>Camellia oleifera</i>
<i>Castanopsis carlesii</i>
<i>Castanopsis eyrei</i>
<i>Castanopsis sclerophylla</i>
<i>Castanopsis tibetiana</i>
<i>Cyclobalanopsis gracilis</i>
<i>Lithocarpus hancei</i>
<i>Phoebe shearei</i>
<i>Schima superba</i>
East Asian endemics
<i>Cinnamomum japonicum</i>
<i>Cyclobalanopsis nubium</i>
<i>Lithocarpus glaber</i>
<i>Machilus thunbergii</i>

therefore can have major impacts on species turnover, changes in community structure and species composition and the maintenance of biological diversity and is vital to understanding of the vegetation dynamics of the various degraded forms of EBLF. The subject of resprouting as a mode of vegetation regeneration has been comparatively neglected compared with that of seedbanks and seedling recruitment and only relatively recently has been given close attention (Midgley, 1996; Bellingham and Sparrow, 2000; Bond and Midgley, 2001, 2003; Vesk and Westoby, 2004a,b). Most resprouting research has been related to regeneration after fire in Mediterranean-type shrub and forest communities in Australia and South Africa (Kruger et al., 1997; Kruger and Midgley, 2001; Vesk and Westoby, 2004b). However, the significance of resprouting has been recognised for some EBLF dominant species in Japan (Bellingham et al., 1996; Aiba et al.,

2001; Manabe et al., 2000; Miura and Yamamoto, 2003). Along with Ohkubo et al. (1996) and Vesk and Westoby (2004c), they also introduce the concept of the sprout, shoot or bud bank and emphasise that resprouting can also occur after natural events, such as windblow in typhoons.

In the case of ELBF in China, most disturbance takes the form of forest clearance through cutting for firewood, rather than fire being used or occurring *in situ* as a method of clearance. The intensity of disturbance has often been severe, with mature forest being cleared, but with many stumps remaining and then being allowed to regrow. With the more recent arrival of alternative fuel sources, frequency of clearance is now much reduced. The idea of the ‘persistence niche’, suggested by Bond and Midgley (2001, 2003) to complement the more widely recognised notion of the ‘regeneration niche’ that relates to seedbanks and seedlings, is extremely relevant to EBLF vegetation dynamics. Given the extent of clearance of the former EBLF in China, attempts to restore and conserve the forests must take account of the importance of resprouting in forest regeneration.

1.3. Aims

The first aim was to review the biogeographical status of this neglected forest type and this has already been achieved in the introduction. Secondly, detailed research has been completed into plant community structure in the Tiantong and Dongqian Lake region of Zhejiang province in Eastern China (Fig. 1). Tiantong forest contains a small area of sub-climax mature EBLF, which is close to the original forest in composition, as well as a variety of secondary forest types. In addition, the full range of degraded communities occurs around Dongqian Lake. Thirdly, conservation and management of the remaining forest fragments is a high priority and research is required into the characteristics of these degraded communities with a view to the possibilities for the conservation and restoration of EBLF in China. Understanding of successional dynamics and processes of regeneration is critical to the long-term survival of the forests (Yan, 2003). New research is reported into resprouting patterns within the forests (Wang et al., 2004).

2. Materials and methods

2.1. The study area

The Tiantong/Lake Dongqian study area is located (N29°41′–50′, E121°33′–50′) in Zhejiang province, Eastern China and lies between the east Zhejiang hills and coastal plain (Fig. 2). Tiantong National Forest Park, 28 km south of the city of Ningbo (5 m inhabitants), was created in 1981 and has an area of 349 ha. Although all vegetation is thought to be secondary in character, the mature forests approximate to climax monsoon EBLF partly because areas of forest immediately around a Buddhist temple in the centre of the park are believed to have been protected from complete clearance (Song and Wang, 1995). The environment at Dongqian Lake is very similar to Tiantong. However, the



Fig. 2. The location of Tiantong National Forest Park Reserve and Dongqian Lake near Ningbo in Eastern China.

EBLF in the Dongqian area has been almost completely degraded and thus a representative range of all degraded forest types occurs. The forests in the Tiantong–Dongqian Lake area are managed by the regional forestry agency—the Bureau of Forestry for Ningbo City.

Taibai mountain, in the Tiantong National Forest Park, is the highest peak in this area, at 653 m above sea level, while most other relief is in the range of 100–300 m. With slopes ranging from 20° to over 40°, following forest clearance or disturbance, there is considerable potential for soil erosion. The soils of this area are mainly red and yellow earths (red and yellow ultisols—Buol et al., 1980), with a pH value from 4.4 to 5.1. Contents of calcium, nitrogen, phosphorus, sulphur and manganese are very low. The substrate of parental material is composed of Mesozoic sediments and acidic intrusive rocks, including quartzite and granite. Soils are of variable depth, with a thick humus layer in flatter valley bottoms. Soil texture is mainly medium to heavy loam (Song and Wang, 1995).

The area has a typical monsoon climate with a hot, humid summer and a drier cold winter. The annual mean temperature is 16.2 °C; the warmest month is July with a mean temperature of 28.1 °C, and the coldest is January with a mean temperature of 4.2 °C; the absolute minimum temperature is –8.8 °C. Average annual precipitation is 1374.7 mm, concentrated from May to August (Song and Wang, 1995).

2.1.1. Mature forest species composition

A total of 262 species have been recorded in the EBLF of the Tiantong National Forest Park, belonging to 78 families and 162 genera (Song and Wang, 1995), including ferns: 27 species, 18 genera and 12 families; gymnosperms: 3 species, 3 genera and 3 families; angiosperms: 232 species, 141 genera and 62

families. The vertical structure of the EBLF normally has three layers. The tree layer is 8–20 m high and can be divided into two sub-layers. The first tree layer is >12 m high, coverage is 50–75% and the dominant evergreen broad-leaved trees are *Castanopsis fargesii*, *Castanopsis carlesii*, *Lithocarpus glaber*, *Lithocarpus harlandii*, *Schima superba*, *Cyclobalanopsis glauca*, *Cyclobalanopsis myrsinaefolia*, *Cyclobalanopsis nubium*, *Castanopsis sclerophylla* and *Machilus thunbergii*, mixed with some deciduous trees, such as *Liquidambar formosana*, *Choerospondias axillaris*, *Cyclocarya paliurus*, *Carpinus viminea* and *Diospyros lotus*. The second tree layer is 8–12 m high, coverage is 40–70%, and in addition to the first tree layer species, other common species are *Cinnamomum subavenium*, *Litsea elongata*, *Neolitsea aurata* var. *chekiangensis*, *Photinia glabra*, *Symplocos stellaris*, *Symplocos heishanensis*, *Cleyera japonica* and *Ilex purpurea*. The shrub layer is below 2.5 m; coverage is 25–80%, including *Camellia fraterna*, *Eurya* spp., *Symplocos sumuntia*, *Loropetalum chinense*, *Rhododendron ovatum*, *Vaccinium bracteatum* and *Vaccinium mandarinorum*. The herb layer is below 1 m; coverage is 10–30%, the dominant species are normally ferns, such as *Woodwardia japonica*, *Diplopterygium glaucum* and *Dryopteris* spp. Other common species are *Carex* spp. and *Lophatherum gracile*. There are also lianas in the mature communities, notably *Stauntonia leucantha*, *Morinda umbellata*, *Ficus pumila*, *Trachelospermum jasminoides*, *Parthenocissus tricuspidata*, *Smilax* spp., *Millettia reticulata* and *Dalbergia hancei* (Song and Wang, 1995).

2.1.2. Degraded community composition

Outside Tiantong National Forest Park, including the area around Lake Dongqian, virtually all vegetation is degraded.

Table 2
The provisional seven-stage model of succession in EBLF from Song and Wang (1995)

Stage	Age (years)	Description	Dominant species
1	3	Grass and bush community	<i>C. sclerophylla</i> , <i>Indocalamus tessellatus</i> , <i>Imperata cylindrica</i> var. <i>major</i> , <i>Diplopterygium glaucum</i>
2	10	Secondary shrub community	<i>Quercus fabri</i> , <i>Rubus palmatus</i> , <i>I. cylindrica</i> var. <i>major</i> , <i>Dicranopteris dischotoma</i>
3	20	Coniferous forest	<i>Pinus massoniana</i> , <i>C. sclerophylla</i> , <i>Loropetalum chinense</i> , <i>Rhododendron simsii</i> , <i>D. dischotoma</i> , <i>Dryopteris</i> sp.
4	30	Coniferous and broad-leaved mixed forest	<i>P. massoniana</i> , <i>S. superba</i> , <i>Eurya nitida</i> , <i>Symplocos sumuntia</i> , <i>Carex</i> sp., <i>Dryopteris</i> sp.
5	60	Developing evergreen broad-leaved forest	<i>S. superba</i> , <i>P. massoniana</i> , <i>E. nitida</i> , <i>C. fraternal</i> , <i>Diplopterygium glaucum</i> , <i>D. dischotoma</i>
6	100	Mature evergreen broad-leaved forest (near climax)	<i>S. superba</i> , <i>Castanopsis fargesii</i> , <i>C. fraternal</i> , <i>Eurya japonica</i> , <i>D. glaucum</i> , <i>Woodwardia japonica</i>
7	150	Mature climax evergreen broad-leaved forest	<i>C. fargesii</i> , <i>S. superba</i> , <i>S. sumuntia</i> , <i>C. fraternal</i> , <i>D. glaucum</i> , <i>W. japonica</i>

Plantations of coniferous forest, mostly *Pinus massoniana* and some *Cunninghamia lanceolata* occur widely. The shrub communities are mostly derived from repeat cutting for firewood, while some occur in abandoned tea and tangerine groves. Repeated clear-cutting was formerly commonplace. However, with the advent of natural gas for cooking and heating, the extent of clearance has been significantly reduced in recent decades. Thus many communities have recommenced the early stages of succession, which results in a very diverse mosaic of communities at differing seral stages.

2.2. Methods

2.2.1. Vegetation survey of degraded and successional communities

Within both the Tiantong and Dongqian Lake areas, a total of 199 10 m × 10 m plots were recorded. Spatial sampling was based on initial stratification of the forest and degraded areas into seven main successional types (Table 2), within which samples were taken to describe the maximum variation in the vegetation. Of the 199 plots, 115 were from within the Tiantong Forest and 84 were from the nearby Dongqian Lake area. The vegetation was surveyed between May and November 2002. All vascular plants were identified during each survey. Abundance of each species was estimated on the Braun–Blauquet cover scale (Kent and Coker, 1992).

2.2.2. Environmental, biotic and successional data

At each plot, location and altitude were measured using GPS, along with slope and aspect. Soil depth was estimated according to the records of a National Forestry Resources investigation in 1999, and divided into three classes: 1 = <30 cm, 2 = 30–50 cm, 3 = >50 cm. The distance of each sample point to the nearest stand of mature natural EBLF vegetation, nearest road and closest village were measured by a map available within a local geographic information system. Human impact was also recorded on a 5-point scale using field evidence, including the density of small roads and the number

of cut stumps. Past land use was estimated by asking local people to nominate one of five types of former land use: 1 = natural vegetation; 2 = plantation; 3 = fuel forest; 4 = burned within the past 3 years; 5 = abandoned cultivated land (tea and fruits). The successional stage of each plot was again estimated using the provisional model of Song and Wang (1995) which recognizes seven stages (Table 2).

2.2.3. Data analysis

Two-way indicator species analysis (TWINSPAN) (Hill, 1979; Kent and Coker, 1992) within the PC-ORD computer package (McCune and Mefford, 1999; McCune and Grace, 2002) was used to classify the abundance data from the 199 sample plots, containing 237 species into plant community or species assemblage types.

Analysis of environmental, biotic and successional gradients was achieved using Canonical Correspondence Analysis (CCA) within both the CANOCO and PC-ORD computer packages (ter Braak, 1986, 1987, 1994; McCune and Mefford, 1999; ter Braak and Šmilauer, 2002; Lepš and Šmilauer, 2003). Species abundance data were entered together with 10 environmental/biotic variables. Aspect data were linearised to a north-south range, using the formula $\cosine(180^\circ - x) + 1.1$, where x is the aspect in degrees from north. Sites with no slope and hence no aspect were given a score of 1.1. Scaling was optimized on species and Monte–Carlo tests were applied to both the eigenvalues and the species–environment correlation on each axis. In terms of multiple regression modeling within CCA, after the initial run with 10 environmental/biotic variables, four (distance to nearest road and village, past and present human impact) were eliminated, since they contributed little to the explained variance.

2.2.4. Description and analysis of resprouting characteristics of EBLF species

2.2.4.1. Resprouting characteristics of various communities.

An initial survey of the relative proportions of resprouting to reseeded across all tree and shrub species was also completed

in representative 10 m × 10 m quadrats from 15 of the species assemblage groupings derived from the TWINSpan classification. The number and abundance of stumps, multi-stem and single stem trees in each quadrat was also surveyed.

2.2.4.2. Resprouting in relation to age and successional stage.

Resprouting communities were identified in two ways.

- (1) Study of forest management history records from the local Bureau of Forestry;
- (2) Identification of degraded areas dominated by resprouting trees and shrubs, where regeneration by seed was less important.

On the basis of the above information, four successional stages following clearance were identified for further detailed analysis—at 1, 20, 43 and 60 years. In representative areas of each of the four stages, one 20 m × 20 m quadrat was laid out, plus another 20 m × 20 m quadrat in mature EBLF for comparison. The four non-mature quadrats were all selected from within the Tiantong reserve and were known to have been mature sub-climax EBLF (*C. fargesii* + *C. carlesii* + *S. superba*) before cutting. All quadrats were in a similar physiographic location, with approximately the same aspect, slope angle and mid-slope position. Within the quadrats, every individual tree or shrub over 5 cm in height was identified and recorded in terms of

whether they had grown from a seedling or whether they had resprouted. Each quadrat was also compared with the 7-stage model of succession within this area (Table 2). Resprouting ability of trees and shrubs was assessed by counting the number of resprouts. Virtually all resprouting was as a result of cutting and in some locations, stumps had been cut more than once. This gives rise to the idea of secondary and tertiary resprouting, with resprouting primarily occurring through epicormic buds, although some species, notably *C. fargesii*, *C. fraterna* and *S. superba* do also resprout from underground roots. Most cutting results in multi-stemmed tree/shrub architecture. The logging history of stumps in each community was also estimated both from forest records and from tree coring.

3. Results

3.1. Assessment of plant community structure and environmental, biotic and successional gradients

3.1.1. Plant community types

From the TWINSpan analysis of the degraded/mature forest survey, a total of 22 community types were identified and are grouped into five general physiognomic/forest types in Table 3. A striking feature of the groups is the high species richness in most communities and the typically high mean number of species per plot. Detailed composition of

Table 3

The 22 community types from the TWINSpan analysis of degraded EBLF data at Tiantong and Lake Dongqian and their species richness—plot size 10 m × 10 m

Type of physiognomy	Type of communities	Number of plots	Total number of species in all plots	Mean species richness/plot
1. Shrub	(1) <i>L. chinense</i> – <i>Miscanthus floridulus</i>	5	75	20.33
	(2) <i>I. tessellatus</i>	2	47	8.75
	(3) <i>L. chinense</i> – <i>L. glaber</i>	8	48	15.25
	(4) <i>Vaccinium bracteatum</i> – <i>Symplocos setchuensis</i>	16	73	18.31
	(5) <i>Diospyros kaki</i> var. <i>sylvestris</i> – <i>Liquidambar formosana</i>	8	59	21.75
	(6) <i>S. sumuntia</i> – <i>S. superba</i>	13	54	18.31
	(7) <i>I. tessellatus</i> – <i>Platycarya strobilacea</i>	6	81	24.78
	(8) <i>Mallotus tenuifolius</i> – <i>Dalbergia hupeana</i>	6	82	21.6
2. Conifer forest	(9) <i>L. chinense</i> – <i>P. massoniana</i>	34	117	19.53
	(10) <i>Lindera rubronervia</i> – <i>P. massoniana</i>	5	59	22.8
	(11) <i>L. glaber</i> – <i>S. superba</i> – <i>P. massoniana</i>	11	51	19.09
	(12) <i>M. tenuifolius</i> – <i>L. formosana</i> – <i>P. massoniana</i>	12	81	18.8
	(13) <i>Cinnamomum camphora</i> – <i>Melia azedarach</i> – <i>P. massoniana</i>	8	74	25.5
	(14) <i>Alniphyllum fortunei</i> – <i>Cunninghamia lanceolata</i>	5	65	29.8
	(15) <i>C. lanceolata</i>	5	58	19.83
3. Mixed forest	(16) <i>Broussonetia papyrifera</i> – <i>Celtis tetrandra</i> spp. <i>sinensis</i> – <i>P. massoniana</i>	5	57	22.8
	(17) <i>L. formosana</i> – <i>C. camphora</i> – <i>P. massoniana</i>	6	62	24
	(18) <i>S. superba</i> – <i>P. massoniana</i>	10	54	18.1
4. Deciduous broad-leaved forest	(19) <i>C. tetrandra</i> spp. <i>sinensis</i> – <i>Ulmus parvifolia</i>	5	43	16.6
	(20) <i>L. formosana</i> – <i>P. strobilacea</i>	6	77	26
5. Sub-climax evergreen broad-leaved forest	(21) <i>C. camphora</i> (planted)	4	57	24.75
	(22) <i>C. glauca</i> – <i>S. superba</i>	14	92	21.71

The 22 types are generalised to five main physiognomic groups to assist with later analysis.

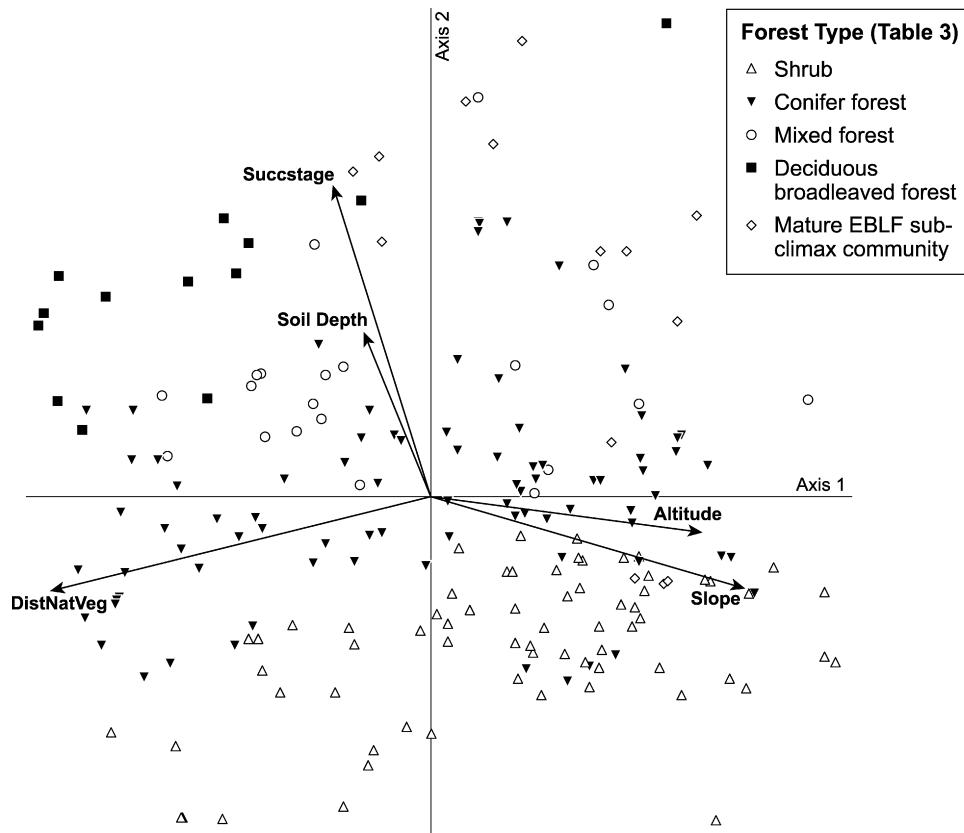


Fig. 3. Sample-environment biplot (axes 1 and 2) from canonical correspondence analysis of the degraded EBLF data from Tiantong and Dongqian Lake (eigenvalues: axis 1 = 0.311; axis 2 = 0.201). Membership of the five physiognomic groups (Table 3) is superimposed.

community types is available from the authors. Only community type 22—the *C. glauca*–*S. superba* community can be seen as mature EBLF and even this is best seen as being in a sub-climax state.

3.1.2. Environmental, biotic and successional gradients

The CCA sample ordination biplot is presented in Fig. 3. The Monte–Carlo tests for both the eigenvalues and the species–environment correlations for each axis were highly significant

($p = 0.001$). The first ordination axis is strongly correlated with distance from nearest mature forest stand ($r = -0.75$), slope ($r = 0.62$) and altitude ($r = 0.53$). Across all forest types, there is an altitudinal-slope gradient from flatter habitat at low altitude to steeper slopes at higher altitudes within the study area, with mature sub-climax forest occurring on higher, steeper slopes. The second axis is very highly correlated with successional stage and disturbance ($r = 0.70$) and also with soil depth ($r = 0.36$). In Fig. 3, the sample plot membership of the

Table 4
The number of individuals resprouting and regenerating as seedlings in 15 of the communities listed in Table 3

Name of community	Sprouting	Seedling	Ratio
(6) <i>S. sumuntia</i> – <i>S. superba</i> comm.	340	44	7.73
(7) <i>I. tessellatus</i> – <i>P. strobilacea</i> comm.	44	50	0.88
(9) <i>L. chinense</i> – <i>P. massoniana</i> comm.	28	100	0.28
(11) <i>L. glaber</i> – <i>S. superba</i> – <i>P. massoniana</i> comm..	52	103	0.5
(12) <i>M. tenuifolius</i> – <i>L. formosana</i> – <i>P. massoniana</i> comm..	33	89	0.37
(13) <i>C. camphora</i> – <i>M. azedarach</i> – <i>P. massoniana</i> comm.	13	81	0.16
(14) <i>A. fortunei</i> – <i>C. lanceolata</i> comm.	9	72	0.13
(15) <i>C. lanceolata</i> comm.	62	23	2.7
(16) <i>B. papyrifera</i> – <i>C. tetrandra</i> spp. <i>sinensis</i> – <i>P. massoniana</i> comm..	0	38	0
(17) <i>L. formosana</i> – <i>C. camphora</i> – <i>P. massoniana</i> comm.	7	60	0.12
(18) <i>S. superba</i> – <i>P. massoniana</i> comm..	86	83	1.04
(19) <i>C. tetrandra</i> spp. <i>sinensis</i> – <i>U. parvifolia</i> comm..	12	48	0.25
(20) <i>L. formosana</i> – <i>P. strobilacea</i> comm.	13	109	0.12
(21) <i>C. camphora</i> comm.	0	61	0
(22) <i>C. glauca</i> – <i>S. superba</i> comm.	61	73	0.84
Overall	760	1034	0.74

five major physiognomic/forest groups of Table 3 have been superimposed and this confirms the clear successional trend with the second axis.

3.2. Resprouting analysis

3.2.1. Overall proportion of resprouting and its distribution among the various communities (based on 10 m × 10 m plots)

Table 4 presents the proportions of individuals regenerating through resprouting, as opposed to regrowth from seed, in 15 of the 22 community types identified in Table 3. Insufficient time had elapsed for estimates of regeneration through seedling regrowth in a number of the early stage communities. While, as would be expected, regrowth via seed is important in all communities, the comparative significance of resprouting in regrowth is clearly demonstrated and the overall ratio of sprouting to reseedling in all 15 communities was 0.74, with 42% of all regeneration via resprouting across all communities. Within this, marked variations occurred. By far the most prolific resprouting community was that dominated by *S. sumuntia*–*S. superba*, with a ratio of resprouting to reseedling of 7.73. However, this is an early shrub stage community. In only two other communities did resprouting actually exceed regrowth via reseedling—the *C. lanceolata* community of the conifer forests and the *S. superba*–*P. massoniana* community of the mixed forests. Nevertheless, resprouting represented a significant regeneration mechanism in a majority of communities.

3.2.2. Resprouting in relation to age and successional stage (based on five 20 m × 20 m plots)

In Table 5, the proportions of regeneration via resprouting or as seedlings in relation to plot age (1, 20, 43 and 60 years) and successional stage within typical mature sub-climax communities previously dominated by *C. carlesii*, *C. fargesii* and *S. superba* at each of these stages are shown. In this former sub-climax community type, the rate of resprout regrowth is extremely rapid, as are associated changes in vertical structure of the forest. The evidence for the dominance of resprouting

over seedling regeneration is clearly demonstrated at all stages, particularly in the tree and shrub layers. As succession proceeds, the proportion of regeneration from the herb layer becomes progressively less, both in terms of resprouting and seedling regrowth. As would be expected, with successional advancement, the overall number of successful resprouts or seedlings is reduced through competition, particularly due to shading from the most rapidly growing tree and shrub species. However, through succession, the proportion of primary resprouts from the first stump increases as a proportion of all resprouting. In the tree layer, although the total number of resprouts progressively falls after 20 years, the proportion of primary resprouting from the first stump increases through the four stages from 23.9% at 20 years to 82% at 60 years. This indicates that the most vigorous and rapid resprout growth occurs from stumps that have only been cut once and these then tend to grow on to dominate in the regenerated community. The proportion of mature trees derived from seedlings is also progressively reduced, so that at 60 years, in the tree layer, a majority of trees (82%) are derived from primary resprouting. In contrast, in the shrub layer, seed regeneration increases through succession, while in the herb layer, the number of individuals regenerating from seed increases up to 43 years but declines significantly at 60 years, presumably due to shading effects.

In Table 6, the proportions of resprouting versus regeneration as seedlings for individual tree and shrub species in relation to plot age (1, 20, 43 and 60 years) and successional stage within typical former mature sub-climax communities dominated by *C. carlesii*, *C. fargesii* and *S. superba* are presented. The dominance of these three main species throughout the secondary regrowth is clearly demonstrated, although the highest number of seedlings is for *Litsea cubeba* but entirely at the initial (1 year) successional stage and it is eliminated by the 20-year stage. Of the 30 species in the table, 10 (*C. fargesii*, *S. superba*, *R. ovatum*, *Camelia fraternal*, *L. glaber*, *S. sumuntia*, *Eurya rubignosa* var. *attenuate*, *Symplocos stellaris*, *Myrica rubra* and *M. thunbergii*) are present at all four ages. Regeneration strategies are comparatively evenly distributed at the first successional stage (resprouting 54.6%; reseedling

Table 5

The number of individuals in three vegetation layers in typical former cleared mature sub-climax EBLF communities (*C. fargesii* + *C. carlesii* + *S. superba*) at each of four stages of regrowth either via resprouting or as seedlings in relation to plot age and successional stage

Stages	Community type	Regeneration mode	Tree (≥5 m)	Shrub (≥1 m)	Herb (<1 m)	Whole community
After 1 year	I	Resprouting (first stump)	–	–	2943 (539)	2943 (539)
		Seedling	–	–	778	778
After 20 years	II	Resprouting (first stump)	473 (113)	159 (26)	615 (109)	1247 (248)
		Seedling	8	21	202	231
After 43 years	III	Resprouting (first stump)	61 (36)	267 (41)	280 (38)	608 (115)
		Seedling	6	63	296	365
After 60 years	IV	Resprouting (first stump)	50 (41)	126 (54)	16 (6)	192 (101)
		Seedling	6	97	209	312

Figures in parentheses are the number of regrowth out of the total for each stage and layer that represent primary resprouting from the first stump following cutting. I: *C. carlesii* + *L. cubeba* + *W. japonica* community—1 year; II: *C. carlesii* + *S. superba*–*Rhododendron ovatum* + *C. fraternal*–*W. japonica* + *Pteridium aquilinum* var. *latiusculum* community—20 years; III: *C. fargesii* + *S. superba*–*R. ovatum* + *Syzygium buxifolium*–*W. japonica* + *Carex* spp. community—43 years; IV: *C. fargesii* + *S. superba*–*C. fraternal* + *S. sumuntia*–*W. japonica* + *D. glaucum* community—60 years.

Table 6

The frequencies of regeneration through either resprouting or regenerating as seedlings for individual tree and shrub species in typical former cleared mature sub-climax EBLF communities (*C. fargesii* + *C. carlesii* + *S. superba*) at each of four stages of regrowth

Species	Regrowth stage								N
	I Resprout %	I Reseed %	II Resprout %	II Reseed %	III Resprout %	III Reseed %	IV Resprout %	IV Reseed	
<i>L. cubeba</i>	3 (1.0)	291 (99.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	294
<i>C. fargesii</i>	38 (69.1)	17 (30.9)	46 (67.6)	22 (32.4)	30 (52.6)	27 (47.4)	23 (46.0)	27 (54.0)	230
<i>S. superba</i>	37 (72.5)	14 (27.5)	32 (56.1)	25 (43.9)	17 (27.9)	44 (72.1)	17 (51.5)	16 (48.5)	202
<i>C. carlesii</i>	124 (96.1)	5 (3.9)	38 (79.2)	10 (20.8)	0 (0.0)	8 (100.0)	0 (0.0)	0 (0.0)	185
<i>R. ovatum</i>	1 (100.0)	0 (0.0)	18 (47.4)	20 (52.6)	29 (27.1)	78 (72.9)	3 (18.8)	13 (81.3)	162
<i>C. fraterna</i>	37 (77.1)	11 (22.9)	9 (34.6)	17 (65.4)	2 (10.5)	17 (89.5)	13 (20.0)	52 (80.0)	158
<i>L. glaber</i>	26 (49.1)	27 (50.9)	22 (62.9)	13 (37.1)	2 (18.2)	9 (81.8)	2 (10.5)	17 (89.5)	118
<i>S. sumuntia</i>	26 (72.2)	10 (27.8)	8 (61.5)	5 (38.5)	6 (18.8)	26 (81.3)	4 (23.5)	13 (76.5)	98
<i>Eurya rubiginosa</i> var. <i>attenuata</i>	19 (82.6)	4 (17.4)	7 (43.8)	9 (56.3)	5 (21.7)	18 (78.3)	7 (23.3)	23 (76.7)	92
<i>Sassafras tzumu</i>	0 (0.0)	87 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	87
<i>Cyclobalanopsis myrsinaefolia</i>	35 (68.6)	16 (31.4)	3 (37.5)	5 (62.5)	0 (0.0)	0 (0.0)	0 (0.0)	2 (100.0)	61
<i>Symplocos stellaris</i>	7 (100.0)	0 (0.0)	8 (42.1)	11 (57.9)	1 (11.1)	8 (88.9)	4 (23.5)	13 (76.5)	52
<i>C. camphora</i>	9 (18.8)	39 (81.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	48
<i>Ardisia crenata</i> var. <i>bicolor</i>	12 (31.6)	26 (68.4)	0 (0.0)	3 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	6 (100.0)	47
<i>Neolitsea aurata</i> var. <i>chekiangensis</i>	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2 (22.2)	7 (77.8)	12 (37.5)	20 (62.5)	41
<i>S. buxifolium</i>	1 (100.0)	0 (0.0)	1 (25.0)	3 (75.0)	4 (11.4)	31 (88.6)	0 (0.0)	0 (0.0)	40
<i>C. sclerophylla</i>	10 (35.7)	18 (64.3)	6 (75.0)	2 (25.0)	2 (50.0)	2 (50.0)	0 (0.0)	0 (0.0)	40
<i>Clerodendrum cyrtophyllum</i>	7 (19.4)	29 (80.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	36
<i>Styrax fabri</i>	16 (66.4)	8 (33.3)	0 (0.0)	1 (100.0)	0 (0.0)	7 (100.0)	0 (0.0)	0 (0.0)	32
<i>Choerospondias axillaris</i>	5 (16.7)	25 (83.3)	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	31
<i>Albizia kalkora</i>	2 (6.7)	28 (93.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	30
<i>Myrica rubra</i>	7 (100.0)	0 (0.0)	5 (71.4)	2 (28.6)	6 (100.0)	0 (0.0)	1 (12.5)	7 (87.5)	28
<i>L. chinense</i>	1 (50.0)	1 (50.0)	15 (60.0)	10 (40.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	27
<i>Symplocos heishanensis</i>	0 (0.0)	0 (0.0)	2 (15.4)	11 (84.6)	0 (0.0)	7 (100.0)	0 (0.0)	0 (0.0)	20
<i>Vaccinium mandarinorum</i>	0 (0.0)	0 (0.0)	7 (63.6)	4 (36.4)	0 (0.0)	1 (100.0)	2 (25.0)	6 (75.0)	20
<i>A. fortunei</i>	5 (27.8)	13 (72.2)	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	19
<i>Cinnamomum subavenium</i>	0 (0.0)	0 (0.0)	7 (58.3)	5 (41.7)	0 (0.0)	3 (100.0)	0 (0.0)	4 (100.0)	19
<i>V. bracteatum</i>	2 (40.0)	3 (60.0)	3 (42.9)	4 (57.1)	0 (0.0)	5 (100.0)	0 (0.0)	1 (100.0)	18
<i>M. thunbergii</i>	4 (66.7)	2 (33.3)	0 (0.0)	1 (100.0)	0 (0.0)	5 (100.0)	1 (33.3)	2 (66.7)	15
<i>C. glauca</i>	5 (50.0)	5 (50.0)	1 (20.0)	4 (80.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	15
Number of individual trees/shrubs (all species)	439	679	238	189	106	303	89	222	
Number of species	25	22	19	24	12	18	12	16	
Mean % resprout/reseed	(54.6)	(45.4)	(40.2)	(59.8)	(19.6)	(80.4)	(20.3)	(79.7)	

Figures in parentheses are % of regeneration for each species by either resprouting or reseeded at each stage. I: *C. carlesii* + *L. cubeba* + *W. japonica* community—1 year; II: *C. carlesii* + *S. superba*–*R. ovatum* + *C. fraterna*–*W. japonica* + *P. aquilinum* var. *latiusculum* community—20 years; III: *C. fargesii* + *S. superba*–*R. ovatum* + *S. buxifolium*–*W. japonica* + *Carex* spp. community—43 years; IV: *C. fargesii* + *S. superba*–*C. fraterna* + *S. sumuntia*–*W. japonica* + *D. glaucum* community—60 years.

45.4%) but by Stages III (43 years) and IV (60 years) reseeded is dominant (Stage III: resprouting 19.6%; reseeded 80.4%; Stage IV resprouting 20.3%; reseeded 79.7%). This dominance by reseeded masks important differences between tree and shrub species. There is more regeneration by resprouting in the major upper layer tree species (*C. fargesii*, *S. superba* and *L. glaber*) and a majority of these are from primary resprouts (Table 5), but the bulk of remaining shrub and smaller tree species are reproducing by seed. Hence the dominance of individuals derived from reseeded at Stages III and IV but this is only characteristic of the understorey trees and shrubs and not the upper canopy trees.

3.2.3. Species richness, life form and resprouting

Table 7 presents the species richness of the herb, shrub and tree layers in the four 20 m × 20 m plots at the four stages of resprouting in comparison with mature forest. For the first

stage, herb species richness is highest but falls at the second stage and remains constant thereafter. Shrub richness increases from Stage II to mature forest. In contrast, tree diversity is richest at Stage II and then declines slightly, as dominant

Table 7

Species richness of the resprouting communities at the four stages of secondary succession of Table 5 and in mature EBLF

	Stage				Mature forest
	I	II	III	IV	
Species richness					
Tree layer	–	11	5	7	8
Shrub layer	–	20	21	30	38
Herb layer	78	46	42	47	45
Total ^a	78	51	48	53	54

^a A number of species were present in more than one layer.

Table 8
Changes in the Raunkaier life form spectra of the resprouting communities at the four stages of secondary succession of Table 5 and in mature EBLF

Life form	Successional stages				
	I (%)	II (%)	III (%)	IV (%)	Mature forest (%)
Dph	34.6	19.6	6.2	5.7	5.6
Eph	52.6	66.7	77.1	75.5	74.1
C	0.0	0.0	2.1	1.9	0.0
H	1.3	1.9	2.1	3.8	5.6
G	8.9	9.8	10.4	11.3	11.1
Th	2.6	1.9	2.1	1.9	1.9

Dph: deciduous phanerophytes; Eph: evergreen phanerophytes; C: chamaephytes; H: hemicryptophytes; G: geophytes; Th: therophytes.

resprouting species take over. After a fall in species richness at the second successional stage, overall species richness remains more or less constant through the remaining successional stages (Table 7).

In Table 8, the changing distribution of Raunkaier life forms in the 20 m × 20 m plots across the four stages and in mature EBLF are shown. While evergreen tree and shrub species dominate throughout the succession, deciduous species are important at Stages I and II but are progressively replaced by evergreen species at the later sub-climax stages. A greater proportion of deciduous early stage species are derived from reseedling, while resprouting species are predominantly evergreen, being derived from former EBLF climax species.

4. Discussion

4.1. Community types and gradient analysis of Chinese EBLF degraded forest

From a sample of 199 10 m × 10 m forest plots, numerical analysis using TWINSPLAN has revealed 22 community types primarily within degraded forest but with some mature sub-climax forest. The species richness and diversity of these forest

types is clearly shown (Tables 3 and 7). Detailed knowledge of these types is important, firstly to ensure conservation of the full range of vegetation types and secondly to assist with forest restoration.

CCA ordination has revealed a primary vegetation gradient related to distance from mature forest, altitude and slope. Successional stage, closely related to disturbance, corresponds to the secondary gradient. Aiba et al. (2001) analysed data from EBLF on Yakushima Island, southern Japan, dominated by *C. cuspidata* var. *sieboldii* and *Distylium racemosum*, and following ordination using CCA, found strong relationships between altitude and physiography (first axis) and that secondary forest was not related to altitude, but rather to disturbance (second axis), which is a similar result to that found here. In contrast to the results described here (Table 7), they also found that tree species richness was higher under secondary than in mature forest. Overall species richness of sub-climax and mature Chinese EBLF is generally recognised as being greater than in secondary forest and all Chinese EBLF types show greater species richness than in Japan.

4.2. Resprouting and reseedling in secondary succession

In terms of successional management, resprouting in canopy trees, linked to disturbance following clearance of the forests, is critical to EBLF regeneration and restoration. In degraded communities, a high proportion of forest regrowth of canopy trees is attributable to resprouting and, unlike most other habitat types where resprouting is of significance, it is resprouting following cutting that is important, rather than following fire. In the EBLF, the cutting is predominantly for firewood for domestic and rural/agricultural uses, with the consequence that the material is removed from the site and is burned elsewhere, rather than being burned *in situ*.

The most important idea in terms of EBLF resprouting is that of the persistence niche (Bond and Midgley, 2001). Resprouting is a means of persistence and assists in long-term

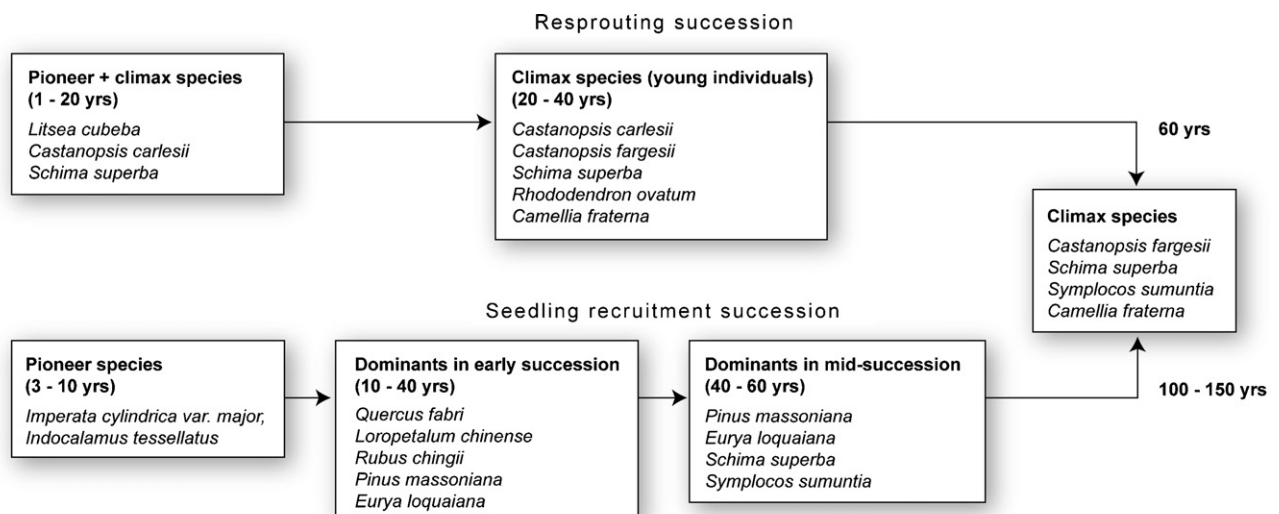


Fig. 4. The relationship between the resprouting and seedling recruitment pathways in EBLF succession in the Tiantong/Dongqian area.

site occupancy. Persistence through resprouting means that resprouting species can remain in the community and speed of regrowth and biomass recovery in secondary succession through resprouting is much faster than would occur via seedlings (Yan et al., 2007). Thus a new model of successional change in EBLF in this part of China is presented (Fig. 4), which shows how dominant species change in both the resprouting and re-seeding secondary successional series. The most important point is that at the first stage, in the first year after cutting, the dominant species are not just pioneer reseeded species but also former mature and climax EBLF species that have regenerated as primary resprouts.

This situation is thus distinctively different from primary succession or secondary succession dominated by reseeded. In Fig. 4, within the reseeded successional series, succession proceeds by several seral stages, through secondary scrub, coniferous and mixed communities to deciduous (Table 3), until the climax species are dominant. This can be described as being closer to the relay floristics model involving autogenic successional processes (Egler, 1954; Li et al., 1999). Resprouting succession is different and can be seen as a 'jump' model, whereby mature and climax EBLF species are still present at the first stage following clearance and thus the community can proceed to a mature sub-climax EBLF community comparatively rapidly within 60 years, as opposed to 100–150 years (Fig. 4). Early and mid-succession stages are omitted. One consequence of this is that dominant canopy tree and shrub species composition can remain quite similar through succession, which agrees with the findings of Li et al. (1999), working in similar forest types in Eastern China. However, overall shrub diversity nevertheless increased through succession in the experimental plots examined at Tiantong (Table 7), which differs from the results of Li et al. (1999). One further aspect is that evergreen broad-leaf tree density remains relatively constant through succession, while shrub density and biomass usually falls as trees mature and cast denser shade (Li et al., 1999). For similar reasons, deciduous trees and shrubs are progressively eliminated as regrowth occurs and succession proceeds (Table 8).

The importance of resprouting in EBLF has previously been reported again from Japan (Bellingham et al., 1996; Aiba et al., 2001; Miura and Yamamoto, 2003). The present study is valuable in that it includes data on resprouting capability in a range of different degraded forest community types (Table 4), and in relation to regrowth in areas previously dominated by mature sub-climax forest, at several stages of forest succession and development (Table 5), together with information on the full range of tree and shrub species (Table 6).

The greater vigour of primary resprouting after tree-shrub cutting, when compared to resprouting after second and third cuts (Table 5) is clearly important in successful re-establishment of mature trees. The potential of resprouting in re-establishment is progressively reduced if successive cuts are made on the same trees.

In EBLF succession in Japan, competitive interaction between resprouters and reseeded individuals has been shown to be critical (Nishimura et al., 2003). Midgley (1996) suggested

that single-stemmed individuals of trees and shrubs from reseeded will be competitively superior to multi-stemmed resprouting species. Whether this occurs among the dominant species of the mature sub-climax and climax Chinese EBLF is not clear. Although multi-stemmed resprouting trees and shrubs appear to succeed in the medium term, the possibility exists that they could eventually be out-competed in the long term by taller single-stemmed individuals derived from seed. Further research into this aspect of regeneration strategies is required.

5. Conclusion

5.1. Implications for EBLF management and conservation and related research

Very few areas of primary EBLF remain in this eastern part of China. Even in reserves, such as at Tiantong, much mature forest is secondary regrowth and forms a sub-climax community. The findings on both the species richness and the importance of the primary and secondary gradients in these remnant forests are of substantial importance if the full spectrum of forest types are to be conserved. In addition to conserving the remnant forests that remain, Chinese ecologists have been concerned to restore suitable areas of degraded forest to former mature and climax types (Ding and Song, 2003; Wang et al., 2001, 2003, 2005). This restoration needs to be informed by ecological theory. The importance of understanding resprouting in secondary succession and its role in greatly speeding up successional processes is critical. In restoration, it is important that firstly, following clearance, stumps of former mature and climax evergreen broad-leaved trees are not removed and can thus be allowed to regenerate via resprouting. Secondly, where stumps have been removed or an area has been subject to multiple cutting, thus weakening the resprouting potential, replanting with mature and climax resprouting tree species is to be encouraged, notably *S. superba*, *L. glaber*, *C. sclerophylla*, *C. fargesii* and *C. carlesii*. Such replanting has been extensively applied in the Dongqian Lake area, with considerable success (Wang et al., 2001, 2003, 2005).

Regeneration of key EBLF trees through seed also requires more detailed investigation. Studies of seed banks and germination success of species are essential to inform forest restoration. Xiao et al. (2005) examined the relationships between seed abundance and seed predation by rodents in *C. fargesii* and further work on both predation and seed dispersal mechanisms and on seedling viability in EBLF trees should be encouraged. More detailed research into competitive interaction between reseeders and single or multiple-stemmed resprouters is also necessary. There is no doubt that, within the wider Chinese EBLF zone, comparative studies of the range of forest types and their dynamics is urgently required before further habitat loss and simplification occurs.

Acknowledgments

Xi-hua Wang wishes to thank National Natural Science Foundation of China for financial support for this research

(Grant No. 30130060). Martin Kent is grateful to both the Royal Society (London) for the award of a Travel Grant and the State Key Laboratory for Coastal and Estuarine Research, East China Normal University, Shanghai, for financial support towards a study visit linked to the EBLF research. Jamie Quinn and Tim Absalom, cartographers, School of Geography, University of Plymouth, kindly drew the figures.

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