Evergreen-Deciduous Broad-Leaved Forest Ecotone in Eastern China: Retrospect and New Perspectives

Song Kun and Da Liang-Jun

Abstract As a transition, the evergreen-deciduous broad-leaved forest ecotone (EDF ecotone) in eastern China occurs between the Yellow River (Huang He) and Yangtze River (Chang Jiang). Due to its wide extent, the EDF ecotone was usually treated as an independent vegetation zone in China. In this chapter, we summarize historical debates about its zonal vegetation and boundaries, and present new perspectives based on a case study that considers effects of topography on the vegetation transition pattern across the EDF ecotone. The case study showed that topographic differentiation in the forest transition pattern from evergreen to deciduous forest occurred in both latitudinal and altitudinal gradients, causing a hierarchical transition process in three dimensions. Based on these results, a mosaic transition pattern across the EDF ecotone is proposed, with more and larger evergreen patches toward the south and more and larger deciduous patches toward the north. This could result in stable mixed evergreen-deciduous broad-leaved forests in the transition areas between evergreen and deciduous patches. Finally, by comparing climate-vegetation relationships in China and Japan, we discuss the formation mechanism of the EDF ecotone and offer a new proposal for its boundary determination, based on these new perspectives.

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EDF Ecotone: Location, Zonal Vegetation and Debates

Location and Boundary

The evergreen-deciduous broad-leaved forest ecotone (EDF ecotone) in eastern China is the transition area between evergreen and deciduous broad-leaved forests in eastern China, which occurs between the Yellow River (Huang He) and Yangtze River (Chang Jiang). Due to its wide extent, the EDF ecotone was usually treated as an independent vegetation zone in China (Fig. 1). In the "Vegetation of China" (Wu 1980) and most other references (Sun 1998; China Vegetation Map Editorial Committee 2001), its southern boundary of the ecotone was assigned to around 31° N in the east and considered to reach Ta-Pa Mountain in Sichuan (southwestern China) via the south slope of Mt. Shennongjia; its northern boundary was considered consistent with a line defined by the Qinling Mountains and Huaihe River. Another viewpoint (Song 1999; Fang et al. 2002), in particular, extended the northern EDF ecotone boundary to near 35° N, making its range in the east twice as wide as in the previous scheme (Fig. 1).

Basically, the EDF ecotone is caused by the transition in broad-leaved forests from dominance by evergreen trees to dominance by deciduous trees. So the ranges of the main evergreen broad-leaved trees determine the boundary of the EDF ecotone. In East Asia, previous studies indicated that the northern and upper limits of evergreen broad-leaved trees and forests were related to low temperatures, which were usually represented by the Kira Warmth Index (WI) value of 85 °C · months (sum of monthly mean temperatures above 5 °C) and the Coldness Index (CI) value of −10 °C · months (sum of monthly mean temperatures below 5 °C). Sometimes the limit was seen as related, in subtropical and warm-temperate regions, to a value of −1 °C for the mean temperature of the coldest month (Ohsawa 1990). In China, though, the northern boundary of the evergreen broad-leaved forest zone is close to a CI value of −2 °C · months and a WI value of 135 °C · months (Song 1999); it does not reach the CI limit near −10 to −15 °C · months (Deng et al. 1985; Fang 1999). So it was suggested that moisture conditions restricted the northward distribution of evergreen broad-leaved forests in China (Fang and Yoda 1991; Fang et al. 2002). Over the past 5000 years, the boundary of the EDF ecotone varied with the shifting of the evergreen broad-leaved forest due to climatic changes. The southern boundary was near 35° N during the warmest periods and approached 29° N during the coldest periods (Liu 1992).

Zonal Vegetation

All debates about the boundaries of the EDF ecotone are related to various perceptions of zonal vegetation and zonal classification (Table 1). In most references, mixed evergreen-deciduous broad-leaved forest was used as the name of the

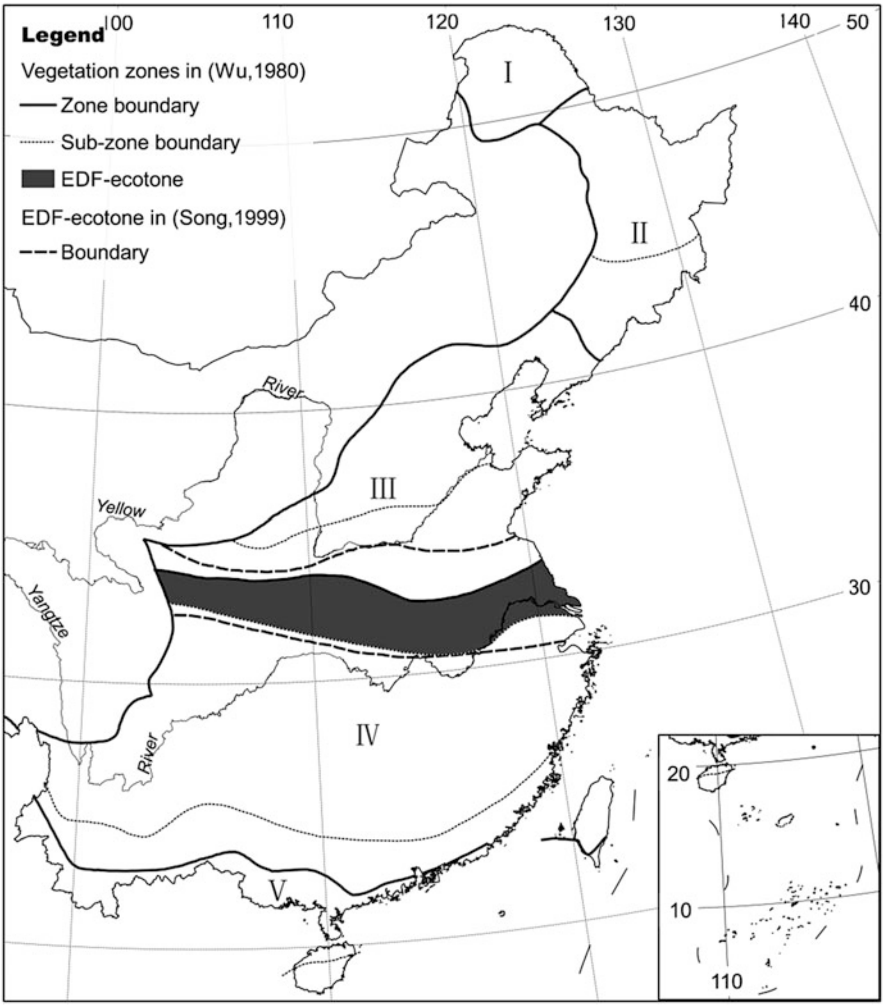

Fig. 1 Location of the EDF (evergreen-deciduous) ecotone in the vegetation zones of eastern China, according to the *Vegetation of China* (Wu 1980). I, cool-temperature coniferous forest zone; II, temperature mixed coniferous and deciduous broad-leaved forest zone; III, temperature deciduous broad-leaved forest zone; IV subtropical evergreen broad-leaved forest zone; V tropical rainforest and monsoon forest zone. Boundaries of the EDF ecotone in Song (1999) are also shown on this map

zonal vegetation in the *Vegetation of China* (Wu 1980), which emphasized the co-domination of the forests by evergreen and deciduous broad-leaved trees (DBT) (Han 1981). In this sense, the EDF ecotone was considered to be a sub-zone of the evergreen broad-leaved forest zone, which belongs to the subtropical climatic zone in the official Chinese zonation system (Wu 1980). On the contrary, a few researchers considered that, in the EDF ecotone, the canopy was dominated by

Table 1 Summary of viewpoints on vegetation and zonation of the EDF ecotone

Zonal vegetation	Vegetation zone	Climatic zone
Deciduous broad-leaved forest with evergreen broad-leaved trees in shrub and herb layers	Mixed deciduous-evergreen broad-leaved subzone in deciduous broad-leaved forest zone	Warm-temperate zone
Dominated by deciduous broad-leaved trees and evergreen elements just occurring in better hydrothermal conditions	Mixed deciduous-evergreen broad-leaved forest zone	
Forest co-dominated by evergreen and deciduous broad-leaved trees	Mixed evergreen-deciduous broad-leaved forest subzone in evergreen broad-leaved forest zone	Subtropical zone

deciduous trees and that evergreen broad-leaved woody plants occurred only in the shrub or herb layers (Qian et al. 1956). This assigned the ecotone as a sub-zone of the deciduous broad-leaved forest zone, which belongs to the 'warm-temperate' climatic zone in the Chinese system (Zhou 1981). In recent decades, based on regional biocoenosis assemblage and vegetation-climate relationships, some researchers (Song 1999; Fang et al. 2002) regarded the EDF ecotone as an independent vegetation zone belong to the warm-temperature zone and named it the mixed deciduous-evergreen forest, representing dominance by deciduous trees in the EDF ecotone (Fang et al. 2002).

Another issue tightly bound with the zonal vegetation of the EDF ecotone was the concept of mixed evergreen and deciduous broad-leaved forest (MEDF; cf. Eyre 1968), which was an independent vegetation type in most vegetation classification systems in China (e.g. Wu 1980) and was considered to be the climax vegetation in the EDF ecotone (Song 1999). This MEDF, however, can also occur in the evergreen broad-leaved forest region on specific topography or edaphic conditions, such as in ravines, on limestone, and in middle altitudes of mountains (Song 2011). Furthermore, the MEDF would be a disclimax vegetation type in the evergreen broad-leaved forest region under frequent, intense disturbance (Song 2011). Natural forests in the EDF ecotone region have been destroyed almost completely, and remnant natural forests are preserved only in mountain regions with extensive secondary forests. Therefore, the boundary and zonal vegetation of the EDF ecotone were distorted, and the formation mechanisms of the MEDF were misunderstood. Even now, it is still hard to distinguish which MEDF could be the climax vegetation in the EDF ecotone. Within the EDF ecotone in eastern China, a formation dominated by *Quercus variabilis* var. *brevipetiolata*, *Castanopsis sclerophylla* and *Cyclobalanopsis glauca* was commonly recorded as the climax MEDF (Liu 1992), but it can also be found in the altitude gradient of typical subtropical mountains. Meanwhile, in last two decades, patches of evergreen broad-leaved forest were recorded in some regions that were considered to be dominated by MEDF, causing a discussion about the local zonal vegetation and leading to various new schemes about the boundaries of the EDF ecotone, such as the Dabie-Shan Mountains in Anhui (Shan and Liu 1964; Han 1981; Deng et al. 1985; Han 1990; Shen 1989).

In conclusion, all debates about the EDF ecotone originated from little knowledge about how evergreen broad-leaved forests are replaced by deciduous forests with increasing latitude and how evergreen and deciduous broad-leaved trees coexist at different spatial scales in the EDF ecotone, especially the assemblage pattern of evergreen and deciduous trees in the mixed forests (MEDF). So, to resolve these questions, we conducted a study in 2010–2011, in Anhui (eastern China), where the zonal vegetation changes from evergreen to deciduous broad-leaved forest. In this study, we evaluated the vegetation transition pattern across the EDF ecotone on different topographies, which have been documented as affecting vegetation distribution greatly at fine scale but without knowledge of effects on vegetation transitions at regional scale.

Transition Pattern Across the EDF Ecotone: A Case Study in Anhui

Study Region and Methods

Anhui Province (29°22′ N–34°40′ N, 114°53′ E–119°30′ E) was a hotspot in debates on the EDF ecotone. Conditions change from a subtropical monsoon climate in the south to a warm-temperate monsoon climate in the north, with mean annual temperature from 14 to 16 °C and average annual precipitation from 750 to 1700 mm. The species composition and community structure of natural forests were compared in three mountain regions, namely the Guniujiang Mountains, Dabie-Shan Mountains, and Huang Cangyu Mountains. These mountain areas belong to the evergreen broad-leaved forest zone, the EDF ecotone, and the deciduous broad-leaved forest zone, respectively (Editorial Committee for Vegetation of Anhui 1981).

We set up 18 plots, 17 plots and 12 plots, respectively, in the basal belt (below 600 m elevation) in the Guniujiang, Dabie-Shan and Huang Cangyu mountains. Each plot was 20 m × 20 m and divided into four subplots. All trees taller than 1.5 m were identified and recorded, and the diameter at breast height (DBH, 1.5 m above ground) and height were measured. Individuals shorter than 1.5 m were also identified, measured by height, and counted for further analyses. All plots were grouped into three topographies: upper slope, lower slope and river valley, according to the topography classification of Nagamatsu and Miura (1997).

A relative importance value (IV) was used to evaluate dominance and was calculated as the mean of relative density, relative frequency and relative basal area at 1.5 m height. To analyze plant trait-environment relationships, rare species were excluded in two ways: (1) species with maximum IV less than 5 % were excluded; and (2) species with frequency less than 5 % were excluded. In total, 7 functional traits and 16 environmental variables were collected in this analysis (see details in Table 2). Functional traits were measured by following Cornelissen

Table 2 Pearson correlations between environmental variables and plant traits on different topographies, using the fourth-corner statistic (combination of models 2 and 4, after (Dray and Legendre 2008)) at community level, weighted by species abundance

		Temperature variables								Precipitation variables					Soil variables		
		MTCQ	CI	PET_{min}	ART	TSN	MAT	WI	PET	PDQ	MAP	Im	AWD	PSN	SoilN	SoilP	SOMC
Upper hillslope	WD	**−0.58**	**−0.57**	**−0.59**	**0.36**	**0.35**	**−0.40**	**−0.33**	**−0.24**	**−0.52**	**−0.50**	**−0.46**	**−0.47**	**0.47**	**0.23**	0.19	−0.06
	N_{mass}	**−0.59**	**−0.58**	**−0.59**	**0.35**	0.33	**−0.43**	**−0.35**	**−0.26**	**−0.52**	**−0.49**	−0.46	−0.45	0.46	0.18	0.21	−0.08
	P_{mass}	**−0.61**	**−0.60**	**−0.61**	**0.39**	**0.36**	**−0.42**	**−0.33**	**−0.24**	**−0.55**	**−0.52**	**−0.50**	−0.49	0.49	0.19	0.23	−0.12
	LL	**0.51**	**0.50**	**0.49**	**−0.31**	−0.28	**0.37**	**0.30**	**0.22**	**0.44**	0.40	0.39	0.39	−0.39	−0.15	−0.22	0.09
	SLA	−0.31	−0.30	−0.30	0.15	0.12	−0.27	**−0.23**	**−0.19**	−0.24	−0.22	−0.20	−0.19	0.20	0.11	0.17	−0.02
	LA	−0.25	−0.24	−0.24	0.15	0.13	−0.19	−0.16	−0.12	−0.22	−0.21	−0.20	−0.19	0.19	0.12	0.15	−0.05
	LDMC	0.38	0.37	0.37	−0.20	−0.20	**0.28**	**0.24**	**0.19**	0.31	0.29	0.27	0.30	−0.30	−0.12	−0.05	0.03
Lower hillslope	WD	**−0.43**	**−0.43**	**−0.43**	0.34	0.30	**−0.35**	**−0.26**	−0.19	−0.37	−0.36	−0.30	−0.29	0.29	0.21	0.14	0.03
	N_{mass}	**−0.62**	**−0.62**	**−0.64**	**0.64**	**0.62**	**−0.31**	−0.12	−0.01	**−0.67**	**−0.66**	**−0.63**	**−0.63**	**0.63**	0.07	−0.03	−0.30
	P_{mass}	**−0.53**	**−0.53**	**−0.54**	**0.48**	0.46	**−0.33**	−0.19	−0.10	**−0.51**	**−0.50**	−0.46	**−0.49**	**0.48**	−0.03	0.01	−0.27
	LL	**0.44**	**0.44**	**0.45**	**−0.44**	−0.39	**0.28**	0.17	0.09	**0.46**	**0.44**	0.40	0.39	−0.39	0.01	−0.19	0.16
	SLA	**−0.55**	**−0.55**	**−0.57**	**0.63**	**0.64**	−0.19	0.00	0.11	**−0.65**	**−0.65**	**−0.64**	**−0.64**	**0.64**	0.01	−0.13	**−0.37**
	LA	**0.44**	**0.44**	**0.45**	**−0.49**	**−0.53**	0.12	−0.03	−0.12	**0.51**	**0.52**	**0.51**	**0.54**	**−0.54**	−0.02	0.18	0.33
	LDMC	**0.49**	**0.50**	**0.51**	**−0.57**	**−0.60**	0.14	−0.03	−0.13	**0.59**	**0.59**	**0.59**	**0.61**	**−0.61**	0.10	0.17	**0.42**

Significant results are in boldface

MTCQ mean temperature of the coldest quarter, *CI* coldness index, PET_{min} minimum monthly potential evapotranspiration, *ART* annual range of temperature, *TSN* temperature seasonality, *MAT* mean annual temperature, *WI* warmth index, *PET* potential evapotranspiration, *PDQ* precipitation of the driest quarter, *MAP* mean annual precipitation, *Im* moisture index, *AWD* annual water deficit, *PSN* precipitation seasonality, *SoilN* total soil nitrogen, *SoilP* total soil phosphorus, *SOMC* soil organic matter content, *WD* woody density, N_{mass}/P_{mass} leaf nitrogen/phosphorus content per dry mass, *LL* leaf life span, *SLA* specific leaf area, *LA* leaf area, *LDMC* leaf dry matter content

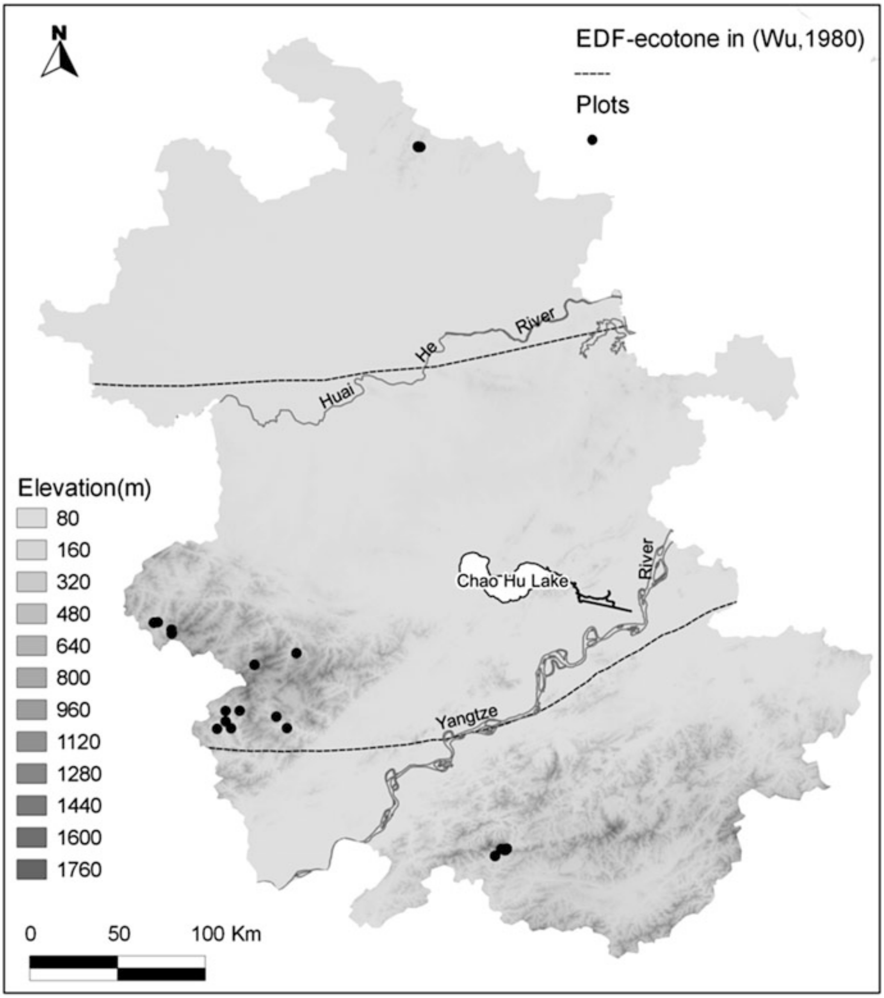

Fig. 2 Location of study sites (*solid circles*) and the boundary of the EDF ecotone (*dashed line*) in Anhui Province, eastern China, adapted from the *Vegetation of China* (Wu 1980)

et al. (2003). Climate variables were calculated based on the WorldClim database, a global climate database with a spatial resolution of 30 arc sec (Hijmans et al. 2005). To quantify the relationship of plant traits and environmental variables, we used the fourth-corner statistic. The significance of correlations was tested with 999 permutations using two different permutation models (Dray and Legendre 2008), with the 'ade4' library (Dray and Dufour 2007) in open-source R (R Core Team 2012) (Fig. 2).

Topographic Differentiation of Forest Transition Pattern Across the EDF Ecotone

In all, 195 woody plant species in 113 genera and 55 families were identified. Most species were broad-leaved trees, except for three evergreen conifer species: *Pinus massoniana*, *Cunninghamia lanceolata* and *Cephalotaxus fortunei*. There were distinctly different transition patterns between upper and lower hillslopes across the EDF ecotone. From south to north, dominance by evergreen trees decreased faster on upper slopes than on lower slopes, while dominance by deciduous trees increased faster on upper slopes than on lower slopes (Fig. 3). In the EDF ecotone, evergreen trees could dominate on the whole slope in the southern Dabie-Shan but just barely on lower slopes in the northern Dabie-Shan. This asynchronous transition pattern on different topographies produced a broad mosaic EDF ecotone filled by both evergreen and deciduous broad-leaved trees.

The turnover of the dominant species was also different on different topographies. On upper slopes, dominance shifted from *Castanopsis eyrei* and *Castanopsis sclerophylla* to *Castanopsis sclerophylla* and *Lithocarpus glaber*, which were replaced finally by deciduous *Quercus* species, such as *Q. variabilis*, *Q. aliena* and *Q. serrata*. On lower slopes, dominance shifted from *Castanopsis eyrei*, *Machilus thunbergii*, *Lithocarpus henryi* and *Cyclobalanopsis glauca* to *Cyclobalanopsis glauca* and *Castanopsis sclerophylla*, which were replaced finally by *Pteroceltis tatarinowii* and *Tilia miqueliana*. This can be summarized briefly as follows: *Castanopsis* and *Cyclobalanopsis* are replaced by deciduous trees on upper and lower slopes, respectively. *Cyclobalanopsis* species were more tolerant to cold than *Castanopsis* species. In eastern China, the coldness limit of *Castanopsis sclerophylla* is near a CI value of -8 °C · month, which makes it weaker than *Cyclobalanopsis gracilis*, with CI limit at -15 °C · month (Deng et al. 1985). In Japan, the northern limit of *Castanopsis* trees is close to the 2 °C isotherm for the mean of the coldest month (Ohsawa et al. 1985), which is higher than the -1 °C northern limit of evergreen broad-leaved forest (Ohsawa 1990). Thus, *Castanopsis* species are replaced by deciduous trees further south than are *Cyclobalanopsis* species, which was the reason for the asynchronous transition patterns on different topographies.

Differentiation in forest transition patterns is caused by different vegetation-climate relationships on different topographies. Previous study suggested that temperature was the major driving factor on upper slopes, especially those aspects related to minimum temperatures, while precipitation seemed to be the main driving factor on lower slopes (Song et al. 2014). This was supported by the plant trait-environment relationships apparent at community level (Table 2). As temperature variables, indices for cold stress, such as mean temperature of the coldest quarter, CI and minimum monthly potential evapotranspiration (PET_{min}), were related more to plant traits than were indices of annual temperature conditions. It was shown also that leaf traits had higher correlation with temperature variables than with precipitation on upper slopes, but the relationship was reversed on lower

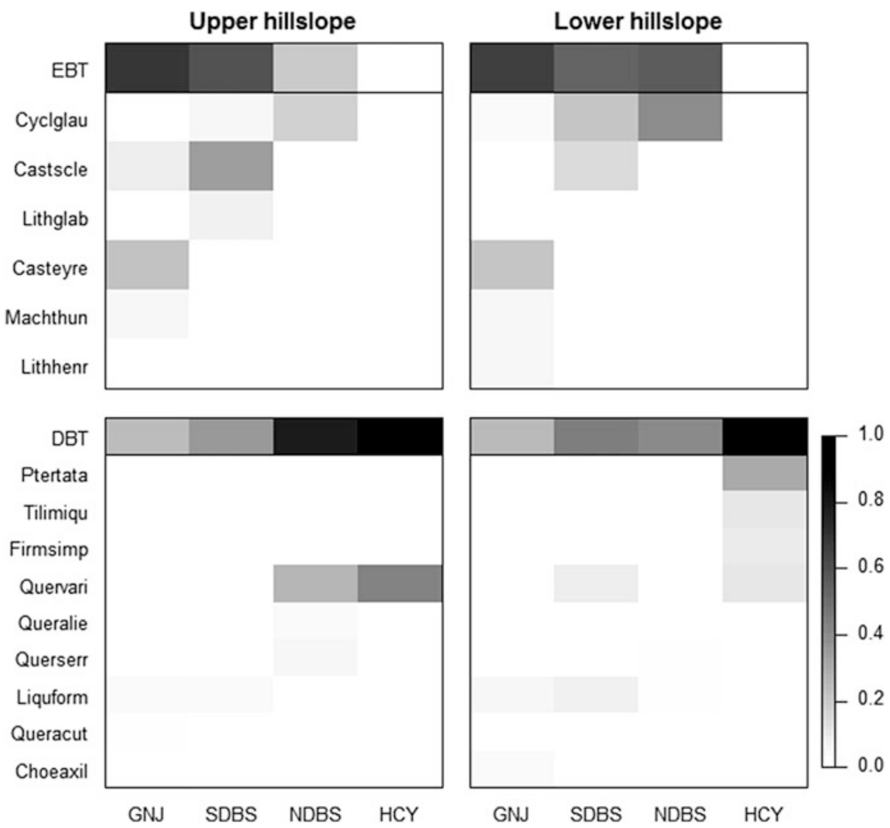

Fig. 3 Variation of importance values (IV) from south to north for evergreen broad-leaved trees (EBT) and deciduous broad-leaved trees (DBT) on upper and lower hillslopes, in Anhui Province. GNJ = Guniujiang Mountain, SDBS = south slope of Dabie-shan Mountains, NDBS = north slope of Dabie-shan, HCY = Huang Cangyu Mountain. Bigger IV values are shown by *darker gray* levels. Upper hillslopes included upper side slopes (USS), and lower hillslopes, including lower side slopes (LSS) and river beds (RB) (Nagamatsu and Miura 1997). Species abbreviations: Cyclglau = *Cyclobalanopsis glauca*, Castscle = *Castanopsis sclerophylla*, Lithglab = *Lithocarpus glaber*, Casteyre = *Castanopsis eyrei*, Machthun = *Machilus thunbergii*, Lithhenr = *Lithocarpus henryi*. Ptertata = *Pteroceltis tatarinowii*, Tilimiqu = *Tilia miqueliana*, Firmsimp = *Firmiana simplex*, Quervari = *Quercus variabilis*, Queralie = *Quercus aliena*, Querserr = *Quercus serrata*, Liquform = *Liquidambar formosana*, Queracut = *Quercus acutissima*, Choeaxil = *Choerospondias axillaris*

slopes (Table 2). On the other hand, on lower slopes, climate was correlated significantly with specific leaf area, leaf area, and leaf dry matter content. This reflects resource allocation in leaves and is closely related to available water, as has been documented many times (e.g. Cornelissen et al. 2003; Markesteijn et al. 2011). On lower slopes, woody plants showed shorter leaf life spans and allocated less of their resources to leaves with decreasing temperature and precipitation, but only shorter leaf lifespans were apparent on upper slopes. This could be because upper slopes are drier and more infertile than lower slopes (Enoki et al. 1996; Hara et al. 1996), and woody plants are prone to have more conservative strategies, such as thicker, smaller leaves with higher dry-matter content. So, woody plants may preserve similar resource allocation strategies in leaves on upper slopes across the EDF ecotone.

Mountain Mixed Forests Caused by Two-Dimensional Transition in the EDF Ecotone

Forests showed the same transition pattern from evergreen to deciduous broad-leaved forest with increasing altitude. The break points in the transition were different, however, on different topographies (Fig. 4). On upper slopes below 350 m, evergreen broad-leaved trees dominated in each vegetation layer, except that the conifer *Pinus massoniana* occurred in the emergent layer in a few plots. Above 350 m, the forest was dominated by deciduous trees, with evergreens under the canopy. A similar shift in forest structure was evident on lower slopes, but the break point was near 500 m. In river valleys the break point could be above 600 m. So it appeared that the altitude of the transitions increased from low upper slopes to high river valleys, which was related to the distribution of three dominant species, *Cyclobalanopsis glauca*, *Castanopsis sclerophylla* and *Quercus variabilis*, on the different topographies and latitudes (Fig. 5). *Castanopsis sclerophylla* occurred mostly below 350 m, and its density and height increased from river valleys to upper slopes. *Cyclobalanopsis glauca* occurred widely in the EDF ecotone but had higher density and larger individuals on lower slopes. *Quercus variabilis* occurred mostly above 350 m and had higher density and more large individuals on upper slopes. Therefore, the break point was near 350 m on upper slopes, where *Cyclobalanopsis glauca* replaced *Castanopsis sclerophylla* as the dominant evergreen tree, but most individuals were small, growing under the canopy constituted by *Quercus variabilis*. Due to the preference of *Cyclobalanopsis glauca* for lower slopes, the break points occurred at higher altitude on lower slopes and highest in river valleys.

With increasing elevation, the dominance of evergreen trees in the canopy decreased gradually and that of deciduous trees increased, beyond the range of *Castanopsis sclerophylla*. This was also caused by different habitat preferences by *Quercus variabilis* and *Cyclobalanopsis glauca* (see above descriptions). *Quercus variabilis* had a low germination rate in stands with wet soil and thick litter layer, and the growth rate of its seedlings showed a negative relationship with soil moisture (Ma et al. 2010). Lower slopes have higher soil moisture and accumulate more litter, which limits the establishment of *Quercus variabilis*. On the other hand, despite having a low germination rate and high mortality among seedlings, *Cyclobalanopsis glauca* showed great sprouting ability in all size classes (Song 2012), which could maintain its population on lower slopes through continuous recruitment.

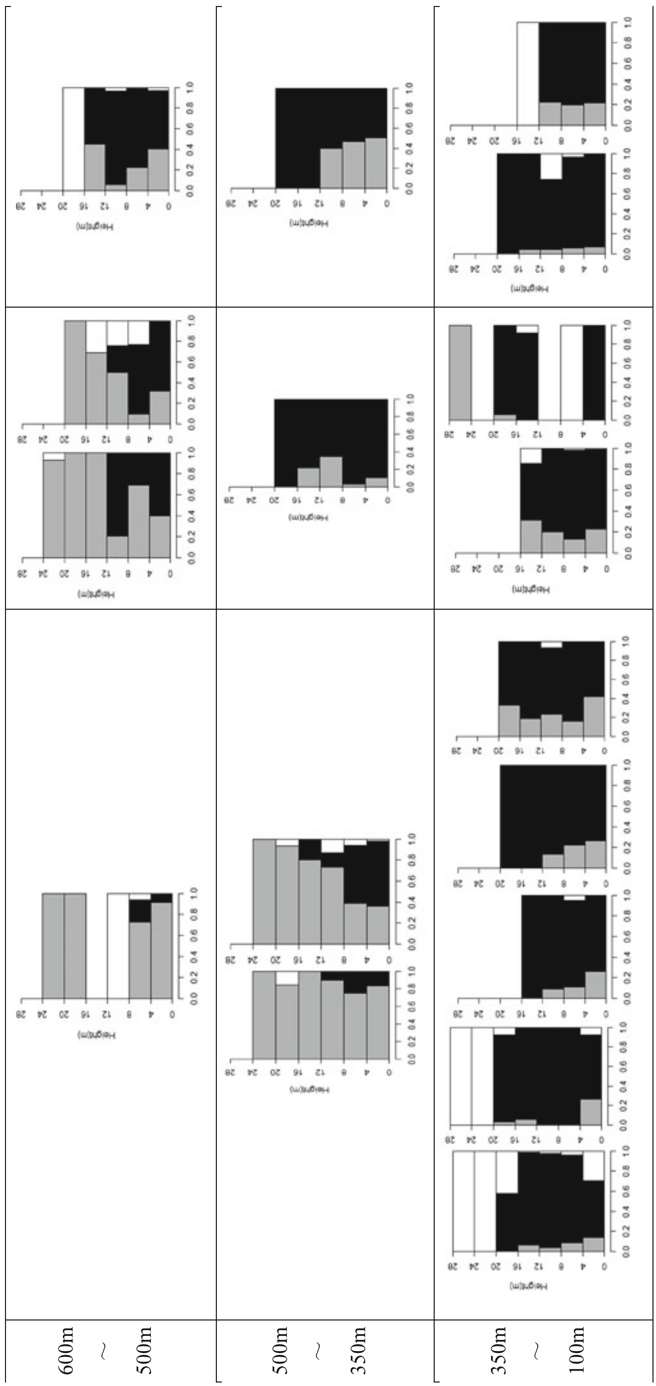

Fig. 4 Height distribution of relative basal area (RBA) for forests on different topographies in the EDF ecotone. Evergreen broad-leaved trees (EBT) are shown in *black*, deciduous broad-leaved trees (DBT) are in *gray*, and evergreen conifer trees are in *white*. *UUS* upper side slopes, *LSS* lower side slopes, and *RB* river beds

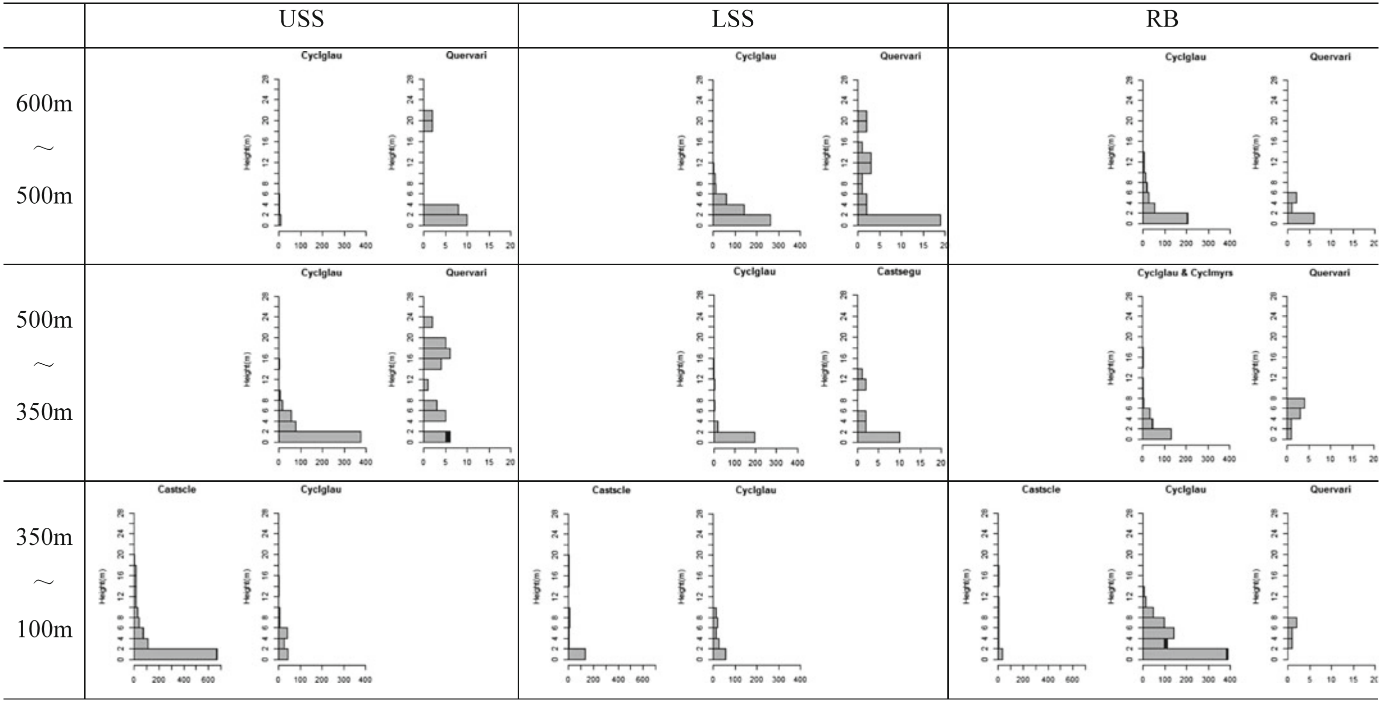

Fig. 5 Height frequency distribution of *Cyclobalanopsis glauca* (Cyclglau), *Castanopsis sclerophylla* (Castscle) and *Quercus variabilis* (Quervari) on different topographies in the EDF ecotone. Living individuals are in *gray*, dead individuals are in *black*. The horizontal axis is the individual number per 0.04 ha. *USS* upper side slopes, *LSS* lower side slopes, and *RB* river bed. Cyclmyrs: *Cyclobalanopsis myrsinifolia*, Castsegu: *Castanea seguinii*

It appears from these observations that evergreen and deciduous broad-leaved trees would probably mix and co-dominate the forests of the transition area along altitudinal and topographic gradients. These forests could be the typical 'mixed evergreen-deciduous forest' (MEDF, or the 'semi-evergreen broad-leaved forest' of other authors, e.g. Eyre 1968) in the EDF ecotone. According to the above results, the co-dominant species of this semi-evergreen forest would be *Quercus variabilis* and *Cyclobalanopsis glauca*. Based on these criteria, two plots on lower slopes at 500–600 m and one plot on an upper slope at 350–500 m were considered to be the typical 'mixed evergreen-deciduous forest'. Each showed a structure in which deciduous trees dominated the canopy and evergreen trees dominated the understory (Fig. 4). By using the mean DBH of the five biggest individuals in each plot, we divided the plots into three stand stages (Fig. 6). Based on the DBH-age relationship established by Zhang et al. (2003) for *Quercus variabilis*, it appears that the youngest stage was about 60 years old, the middle stage about 100 years old, and the oldest stage could be more than 250 years old. With increasing forest age, the two dominant species *Quercus variabilis* and *Cyclobalanopsis glauca* had more large individuals, with continuous recruitment in the 0–20 cm DBH class. Another deciduous tree species, *Platycarya strobilacea*, showed a similar growth pattern. Conversely, two other deciduous tree species, *Quercus serrata* and *Dalbergia hupeana*, had fewer large individuals, and the conifer *Pinus massoniana* had only a few large individuals, without recruitment. All three of these species were inferred to be pioneer species of the evergreen-deciduous forest, as also in the subtropical evergreen broad-leaved forests. We suppose that this would still be a vertically mixed evergreen-deciduous (broad-leaved) forest even if the canopy individuals died, because the pioneer deciduous trees grow faster than does *Cyclobalanopsis glauca* (dashed line in Fig. 6) and the forest would return to the above-described forest dynamics.

Formation Mechanism of the EDF Ecotone and Its Characteristics and Boundaries

Interaction of Climate and Topography Causes the EDF Ecotone

As mentioned in the first section, the values of the coldness index (CI) and warmth index (WI) at the northern boundary of evergreen broad-leaved forest zone in eastern China do not reach the limit for evergreen broad-leaved trees, which were considered to be CI = −10 °C · month and WI = 85 °C · month in subtropical and warm-temperate regions. This means that there is a wide gap between the northern boundary and the temperature limit for evergreen broad-leaved forest in eastern China (Fig. 7a). Theoretically, this gap would be the potential region of the EDF ecotone. By using the WorldClim raster data (Hijmans et al. 2005), we found that

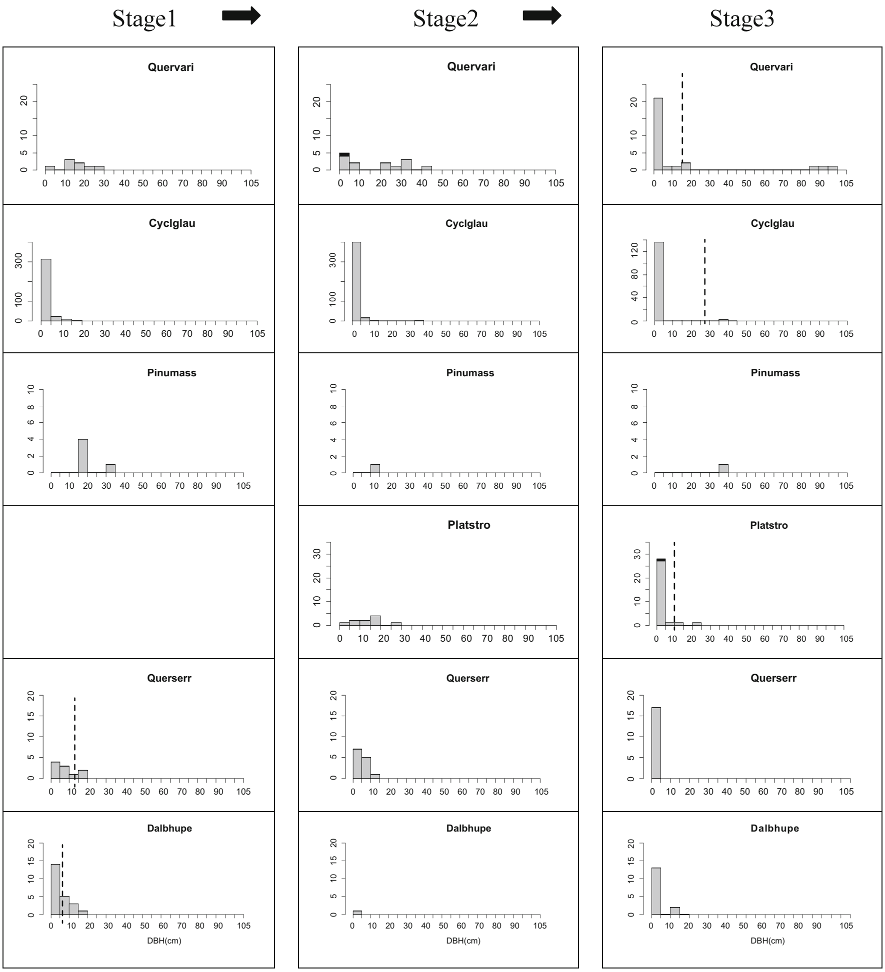

Fig. 6 Frequency distribution of diameter at breast height (DBH) for the main species in forests dominated by *Quercus variabilis* (Quervari) and *Cyclobalanopsis glauca* (Cyclglau), at three stand stages. Living individuals are in *gray*, dead individuals are in *black*. The vertical axis is the individual number per 0.04 ha. The locations of *dashed lines* on the horizontal axis indicate the DBH at which the height was 10 m for each species. Pinumass = *Pinus massoniana*, Platstro = *Platycarya strobilacea*, Querserr = *Quercus serrata*, Dalbhupe = *Dalbergia hupeana*

this gap was almost identical with that of the EDF ecotone in the scheme of Song (1999), after excluding mountain sites in the evergreen broad-leaved forest zone. On the other hand, because the distribution of evergreen broad-leaved forest coincides with its temperature limit in Japan, we presumed limitation of the evergreen broad-leaved forest by precipitation, using the 1 % quantile of the annual precipitation (ca. 1200 mm) of evergreen broad-leaved forest in Japan, wherever CI is higher than −10 °C · month. Excluding mountain sites in the evergreen broad-

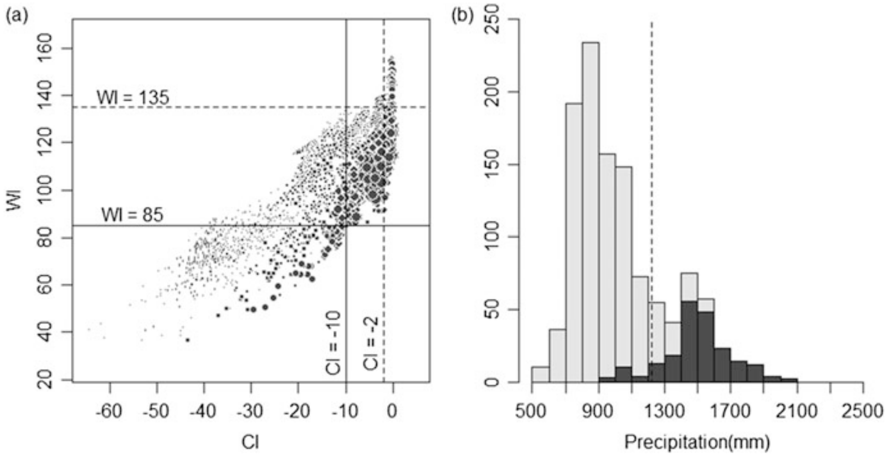

Fig. 7 Warmth Index (WI) and Coldness Index (CI) of the southern part of Eastern China (18–38° N, 105–125° E), based on WorldClim data at 2.5 min resolution (Hijmans et al. 2005). (**a**) Sites located in the *square* surrounded by the four lines of CI = −10, CI = −2, WI = 85, and WI = 135 were considered to be the potential area of the EDF ecotone; its annual precipitation distribution is shown in (**b**). Mountain sites in the evergreen broad-leaved forest zone are in *black* and the others in *gray*. The *dotted line* in (**b**) indicates the 1 % quantile of annual precipitation in the evergreen broad-leaved forest region in Japan, where CI is higher than −10

leaved forest zone showed that more than 90 % of the sites in the potential region of the EDF ecotone have annual precipitation less than the presumed limiting value (Fig. 7b). This supports the idea of a precipitation limit for the northward distribution of evergreen broad-leaved forest (Fang 1999), and so climate appears to be the mechanism for the formation of the EDF ecotone in eastern China.

If only limitation by precipitation were considered, there would be a clear boundary between the evergreen and deciduous broad-leaved forest and the EDF ecotone would be narrow, because precipitation tends to decrease monotonically northward in eastern China. As shown in our study, evergreen broad-leaved forest can occur in the EDF ecotone, and almost all records showed it occurring widely in mountain areas with habitat descriptions such as *located in valley*, *near a stream or river*, or *on humid soil*. Many studies indicated that soil water content was the most distinguishing habitat factor on different topographies, with lower slopes tending to be wetter than upper slopes (Enoki et al. 1996; Hara et al. 1996). These authors pointed out that different soil water availability caused by topography made it possible for evergreen broad-leaved forest to occur in the EDF ecotone and would be another formation mechanism for the EDF ecotone. The effect of topography on soil water content, though, is not unlimited. With decreasing precipitation and lower mountains, there could be a threshold beyond which no topography can provide the soil water needed for evergreen broad-leaved forest. That could be the reason why few evergreen broad-leaved forests were found in hilly regions of the EDF ecotone and why its northern boundary in the *Vegetation of China* (Wu 1980) did not reach the CI = −10 °C · month isotherm.

Characteristics of the EDF Ecotone and Application to Boundary Determination

Based on the study in Anhui and the formation mechanisms of the EDF ecotone, we propose that the basic characteristic of the EDF ecotone is a hierarchical transition from evergreen to deciduous broad-leaved forest along three dimensions: latitude, altitude and topography. For latitude and altitude, the climatic gradient triggers the transition. For topography, redistribution of the fallen precipitation on different topographies results in heterogeneous availability of soil water and nutrients, and seems to be a reasonable explanation for the transition. By this hierarchical transition process, the EDF ecotone would produce a mosaic landscape of evergreen broad-leaved forests and deciduous broad-leaved forests, with more and larger evergreen patches toward the south and more, larger deciduous patches toward the north (see mosaic model below). Stable evergreen-deciduous forests are more likely to occur in the transition areas between evergreen patches and deciduous patches. Because of their greater maximum height and faster growth rate, deciduous trees dominate the canopy and evergreen trees occupy the understory in these evergreen-deciduous forests, which are called vertically mixed evergreen-deciduous forests (MEDF) in this study.

By this mosaic model of the EDF ecotone, the southern boundary should be the threshold where deciduous broad-leaved forest patches occur and the northern boundary should be the threshold where evergreen broad-leaved forest patches disappear completely (Fig. 8). According to our study in Anhui, the shift of dominance from evergreen to deciduous trees with increasing latitude occurred, at lower latitude, on upper slopes more than on lower slopes, which was caused by the replacement of the dominant evergreen species *Castanopsis eyrei* and *Castanopsis sclerophylla* by deciduous species. Therefore, the northern limits of these two species could be considered to be the southern boundary of the EDF ecotone in Anhui. On the other hand, evergreen trees were finally replaced by deciduous trees on lower slopes in the north, due to the replacement of *Cyclobalanopsis glauca* by deciduous species. In the same way, the northern limit of *Cyclobalanopsis glauca* could be considered to be the northern boundary of the EDF ecotone in Anhui.

Application of this boundary determination method can be extended to the whole EDF ecotone. *Castanopsis* species and *Cyclobalanopsis* species can be chosen to determine the southern and northern boundaries, respectively, of the EDF ecotone. As we know, in *Castanopsis*, species with smaller leaves can dominate further north than can other species and can cover almost all the slopes. Their northern limits are suitable markers for the southern boundary of the EDF ecotone. Such species would be *Castanopsis eyrei*, *C. carlesii* and *C. carlesii* var. *spinulosa*. *Cyclobalanopsis* species have the greatest cold tolerance among the evergreen broad-leaved trees, and their northern limits are suitable markers for the northern boundary of the EDF ecotone. In particular, the species involved would be *Cyclobalanopsis glauca* and *C. oxyodon*.

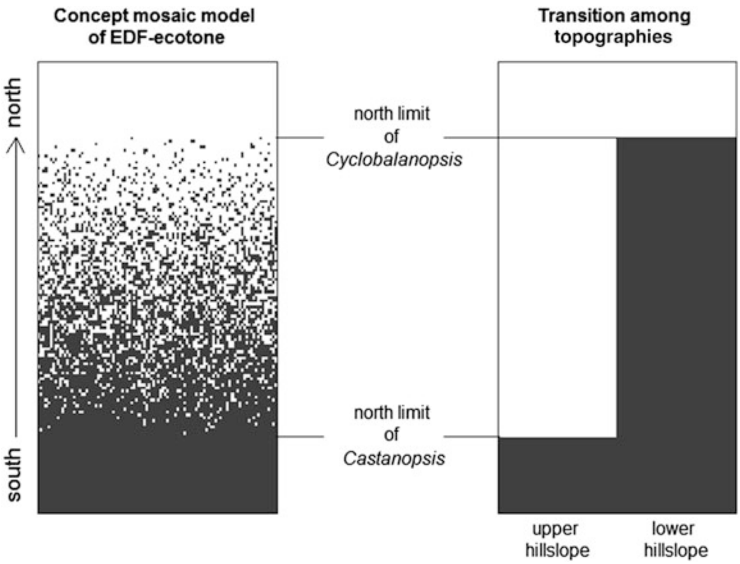

Fig. 8 In the mosaic concept of the EDF ecotone, the southern boundary is consistent with the northern limit of *Castanopsis*, whose dominance is replaced by deciduous broad-leaved trees on upper hillslopes; the northern boundary is consistent with the northern limit of *Cyclobalanopsis*, whose dominance is replaced by deciduous broad-leaved trees on lower hillslopes. The regions dominated by evergreen broad-leaved trees are in *black*, and those dominated by deciduous broad-leaved trees are in *white*

We consider that our method, based on the mosaic concept, is more reasonable than previous boundary determination methods used for the EDF ecotone. The prevalent method using the climate-vegetation relationship ignores the effect of topography on plant distribution, which has been documented in many vegetation zones; it also ignores the clearly different vegetation transition patterns on upper versus lower slopes across the EDF ecotone, as shown in our study. Another prevalent method using relevé records has limited application in eastern China because this region has been exploited intensively and is dominated by secondary forests, most of which are deciduous or evergreen-deciduous forests that can confuse the determination of the EDF ecotone boundaries. Moreover, there are fewer relevé records than floristic records in China. Actually, even for floristic records, most of the distribution data for woody plants were at the county level, across whole provinces and across the whole country (Fang et al. 2011), which seems to be too coarse for checking the boundaries of the EDF ecotone. Even so, we anticipate that this method could determine the boundaries of the EDF ecotone quantitatively and accurately, if there were enough site-based distribution data for the relevant species.

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