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Altitudinal zonation of human-disturbed vegetation on Mt. Tianmu, eastern China

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Abstract Much of the primary vegetation at low altitudes has been greatly altered or destroyed by a long history of human activities. This is particularly true in eastern China, where low-altitude areas are now dominated by secondary forests or plantations. Altitudinal vegetation zonation of this region is often based on these secondary forests, resulting in seral vegetation with an obscure zonal sequence. Here, we deduced the potential climax vegetation according to the regeneration patterns of the dominant species of the secondary forests at low altitudes (below 1,000 m a.s.l.) on Mt. Tianmu (1,506 m a.s.l., 30°18'30"–30°21'37"N, 119°24'11"–119°27'11"E). Based on the potential climax vegetation combined with the floristic composition and community structure, three vegetation zones were identified, viz: (1) evergreen broad-leaved forest zone (400–950 m a.s.l.); (2) ever-

green and deciduous broad-leaved mixed forest zone (950–1,100 m a.s.l.); (3) deciduous broad-leaved forest zone (1,100–1,506 m a.s.l.). The altitudinal vegetation zones identified in this study correspond with the thermal conditions on Mt. Tianmu. The distribution of vegetation on Mt. Tianmu was limited by lower temperatures in winter, and the altitudinal thermal vegetation zones on this mountain were more similar to the thermal vegetation of Japan than to that of China. The vertical distributions and roles of conifers were different between the eastern and the western regions along 30°N latitude in humid East Asia. *Cryptomeria fortunei* formed the emergent layer, towering above the broad-leaved canopy at middle altitudes as *C. japonica* on Yakushima, but disappeared at high altitudes with hydrothermal limitation on Mt. Tianmu.

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Introduction

The division of vegetation zones is an old and highly emphasized topic in both botany and geography. Altitudinal vegetation zonation is one of the most striking gradational patterns of vegetation (Ohsawa 1984). Theoretically, the division of vegetation zones should be based on the climax vegetation. However, much of the primary vegetation at low altitudes has been largely destroyed by historical human activities, particularly in eastern China. In these areas, the vegetation has recovered to secondary forests or plantations due to the policy of vegetation protection by the Chinese government since the late 1970s. If the zones are classified on the basis of the distribution of secondary rather than primary forest, the number of zones decreases and their boundaries become ambiguous (Numata 1966, 1971).

The vegetation of a region can provide information not only about past environmental conditions but also

about a possible future trajectory for the community. Population structure of a species reflects its dominance status and development within the community, whether early successional or climax (Da et al. 2004). Therefore, based on the population structure of each species, it is possible to clarify the regeneration patterns of species, determine the seral stage of the community, and deduce the potential climax vegetation (i.e., those species that would likely occur in the absence of human disturbance) of a particular area. This information will enable a division of the vegetation zones based on potential climax vegetation patterns. We thought this method might represent a feasible way to classify altitudinal vegetation zones under a regime of strong human disturbance in eastern China.

Mt. Tianmu is located in the north subtropical zone, in eastern China. The southern slope of Mt. Tianmu is in the core area of the Mt. Tianmu Nature Reserve. Forests at low altitudes were the principal source of the local people's livelihood in the past. People used the forest for extraction of timber, litter for firewood and livestock bedding, and planted conifers, bamboos and teas for forestry production. Therefore, there is no primary evergreen broad-leaved forest at lower altitudes (below about 1,000 m a.s.l.).

The altitudinal pattern of vegetation on the southern slope of Mt. Tianmu has been studied by several scientists (Feng 1956; Liu 1991; Comprehensive investigation team of Tianmu Mountain nature reserve 1992; Zhou et al. 1992; Chen 1992; Zhang et al. 2003). However, there has been some disagreement about the classification of these patterns, especially for the upper limit of the evergreen broad-leaved forest (Feng 1956; Ai et al. 2004). Here, we divide the altitudinal vegetation zones based on the potential climax vegetation on Mt. Tianmu. Our specific goals are to (1) find a feasible approach to divide altitudinal zones of human-disturbed vegetation in eastern China; (2) research the relationship between distribution of vegetation and thermal conditions, and compare the vertical thermal vegetation zones on Mt. Tianmu with thermal vegetation zones of China and Japan; and (3) compare the vertical distribution of conifers along 30°N latitude in humid East Asia.

Study area and methods

Study site

Mt. Tianmu Nature Reserve (1,506 m a.s.l., 30°18'30"–30°21'37"N, 119°24'11"–119°27'11"E), is located in the Ling'an county of Zhengjiang, the north subtropical area of eastern China, and has a total area of 10.5 km² (Fig. 1). The foothill region is located at 300–350 m a.s.l., which gradually rises to 1,056 m a.s.l. This area is influenced by a monsoonal climate and a high altitude with steep slopes, with heavy rainstorms in the spring and fall, and a large range of snowfall in winter. According to records during 1987 and 1996 from

weather stations at Chanyuan Temple (350 m a.s.l.) near the base and Xianrending (1506 m a.s.l.) near the summit of Mt. Tianmu, the average annual temperature is 14.5 and 9.0°C, and the average annual precipitation is 1,739 mm and 1,751 mm for Chanyuan Temple and Xianrending, respectively (Fig. 2). Mt. Tianmu has a rich flora; the zonal vegetation of this area is evergreen broad-leaved forest (Comprehensive investigation team of Tianmu Mountain nature reserve 1992).

Because the stratum was historically affected by tectonic movements and volcanic activity, the study area is made up of steep slopes and irregular terrain, especially many complex landscape structures between 900 and 1,100 m a.s.l. Ninety percent of Mt. Tianmu is covered with volcanic parent rock (Zhou and Wang 1992). The zonal soils on Mt. Tianmu are comprised of red soils (below 600 m a.s.l.), yellow soils (600–1,200 m a.s.l.) and brown yellow soils (above 1,200 m a.s.l.; Xia 2004).

Methods

Data

Eleven plots were selected to investigate the vertical distribution of vegetation along altitudinal gradients from 400 to 1,506 m a.s.l. on the southern slope of Mt. Tianmu (Fig. 1). Plot size varied from 100 to 2,500 m² due to difficulties in setting up maximum available size with homogeneous topographic habitats (Table S1). Since vegetation was diverse around 1,100 m a.s.l., two plots were chosen: one was a broad-leaved forest and the other was a *Cryptomeria fortunei* forest.

All trees taller than 1.5 m were identified and recorded; the diameter at breast height (DBH at 1.5 m above ground) and height (H) were measured. The layers were discriminated and their heights were measured. The coverage (%) and maximum height of the species of the herb layer were also recorded. Nomenclature follows the Editorial Committee for Vegetation of Zhejiang (1993). This field work was carried out from May 2001 to August 2002.

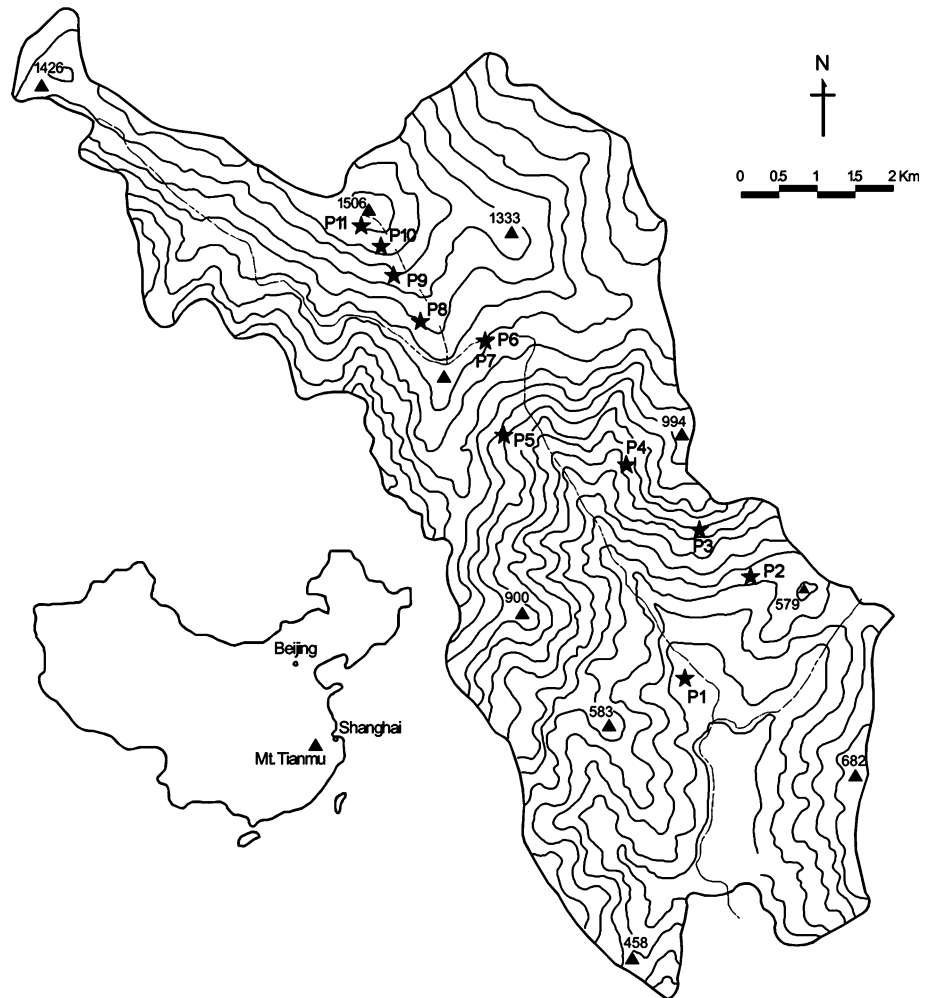
Analyses

Species basal area (BA, cm²) was calculated from the DBH of individual trees. In each plot, relative BA (RBA, %) of each species was used as abundance measure of that species, and the dominant species were determined based on the dominance analysis (Ohsawa 1984).

Population structures of dominant species were shown by DBH class-frequency distributions, which were used to elucidate the regeneration pattern of the species. Based on this, the seral stage of the community and the potential climax vegetation can be ascertained and the altitudinal vegetation zones can then be divided.

The basic structure of vegetation zonation in eastern Asia is largely determined by present climatic condi-

Fig. 1 Location map of the study area. Mt. Tianmu is located in the north subtropical area in eastern China. Topographical map of the study area showing vegetation samplings plots (P1–P11). Asterisks represent the ten study plots along the altitudinal gradient between 400 and 1,506 m a.s.l.



tions, particularly temperature (Ohsawa 1995). We used the warmth index (WI), coldness index (CI), and coldest mean monthly temperature (CMT, Kira 1976) to analyze the relationships between the distribution of vegetation and the thermal conditions on Mt. Tianmu. We estimated the monthly mean temperature lapse rate from the observed climate data from the two weather stations on Mt. Tianmu (1987–1996). Monthly mean temperature and WI and CI were estimated along the southern slope of Mt. Tianmu.

Results

Floristic composition along the altitudinal gradient

Species richness and life-form distribution

There were 152 woody species in 92 genera and 44 families recorded in the ten plots (Table S1), including four evergreen coniferous tree species, one deciduous coniferous tree species, 18 evergreen broad-leaved tree species, 53 deciduous broad-leaved tree species, 12 evergreen broad-leaved shrub species, and 64 deciduous

broad-leaved shrub species. The trend of numbers of family, genus, and species showed a unimodal pattern along altitude, reaching the peak at plot 7 (1,100 m a.s.l.): 37 families, 55 genus, and 72 species. Evergreen conifer species occurred at lower and middle altitudes, reaching the highest RBA of 89.0% in plot 7 (1,100 m a.s.l., Fig. S1). *Pseudolarix kaempferi*, the only deciduous coniferous tree species occurred in plot 7 (1,100 m a.s.l.) with a small RBA. The maximum number of evergreen broad-leaved species (17 species) and the peak RBA (63.6%) occurred in plot 2 (550 m a.s.l., Fig. S1). Evergreen broad-leaved species co-dominated with deciduous species between 710 and 1,220 m a.s.l. (plots 3–6 and plot 8). Deciduous broad-leaved species exhibited similar trends with floristic family, genus, and species richness along an altitudinal gradient, reaching the maximum number of 53 species in plot 7 (1,100 m a.s.l.). Above 1,220 m a.s.l. (plot 8), the number of shrub species was greater than the tree species.

Replacement of species

The forests below 1,100 m a.s.l. were mainly composed of trees of Fagaceae, Lauraceae, and Taxodiaceae, and

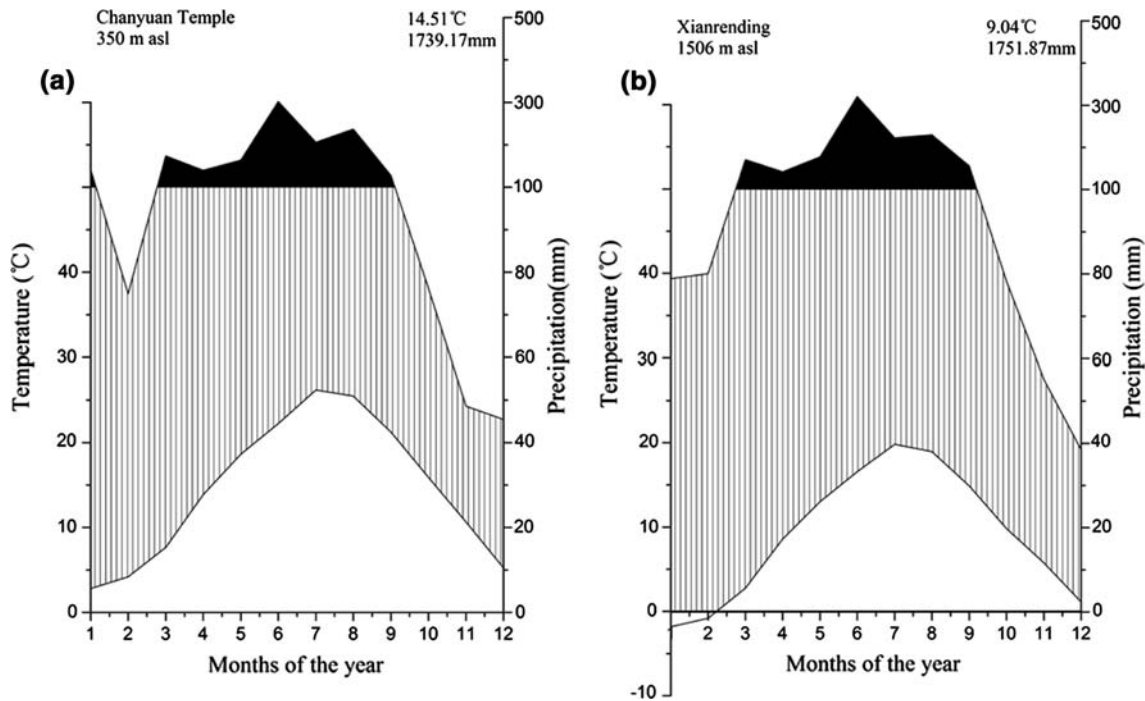


Fig. 2 Walter's climate diagram for Chanyuan Temple (350 m a.s.l.) (a) and Xianrending (1,506 m a.s.l.) (b) of Mt. Tianmu. Data sources are from the weather stations of Mt. Tianmu Nature Reserve (1987–1996)

shrubs of Lauraceae, Theaceae, and Ericaceae, and some dominants of Symplocaceae with a narrower distribution range (Fig. 3). Above 1,100 m a.s.l., forests were mainly composed of trees of Fagaceae and Cornaceae with the narrow-ranging dominants of Taxodiaceae, Daphniphyllaceae, Aquifoliaceae, Betulaceae, and Rosaceae, and shrubs of Rosaceae, Lauraceae, Styracaceae, Caprifoliaceae, and Symplocaceae.

In the foothills, the forest was developed from an abandoned *C. fortunei* plantation. *Phoebe chekiangensis*, *Cinnamomum camphora* (Lauraceae), *Quercus acutissima* (Fagaceae), and *Liquidambar formosana* (Hamamelidaceae) were distributed along the ravine. Around 1,100 m a.s.l. *C. fortunei* forests were distributed as patches of broad-leaved forests.

Fagaceae was the prominent family on Mt. Tianmu (Zhou et al. 1992), showing a vicarious chain distribution ranging from low to high altitudes (Fig. 3). At the lower and middle altitudes (below 1,200 m a.s.l.), evergreen species of Fagaceae were the main components of the climax vegetation. *Castanopsis eyrei* was distributed below 700 m a.s.l., then replaced by *Cyclobalanopsis*. The distribution of the climax species *Cyclobalanopsis gracilis* was wide (550–1,300 m a.s.l.), occurring with *Cyclobalanopsis myrsinaefolia* at low altitudes (below 950 m a.s.l.), *Cyclobalanopsis glauca* at 550–950 m a.s.l., *Lithocarpus harlandii* at 550–1,300 m a.s.l., and co-dominating with *Cyclobalanopsis stewardiana* at middle altitudes (950–1,100 m a.s.l.). Above 1,100 m a.s.l., *Cyclobalanopsis* was gradually replaced by *Quercus glandulifera* var. *brevipetiolata* and *Quercus aliena* var. *acuteserrata*. At high altitudes (around 1,500 m a.s.l.),

Quercus was replaced by *Castanea seguinii*, co-dominating with *Cornus kousa* ssp. *chinensis* and *Cornus controversa* (Cornaceae), *Malus hupehensis* (Rosaceae), and *Lindera rubronervia* (Lauraceae).

Abundant pioneer or seral deciduous species of Fagaceae, Hamamelidaceae, Juglandaceae, Lauraceae and Styracaceae were scattered within the low-altitude evergreen broad-leaved forest in areas affected by human activities. *Sassafras tzumu* (Lauraceae) was a gap regenerating species of *C. eyrei* or *C. gracilis* forests. *Toxicodendron succedaneum* (Anacardiaceae), *Liquidambar acalycina* (Hamamelidaceae), and *Pterostyrax corymbosus* (Styracaceae) occurred with evergreen species around 710–950 m a.s.l. At middle altitudes (840–1,100 m a.s.l.), many Tertiary relict plants occurred, such as *P. corymbosus* (Styracaceae), *Nyssa sinensis* (Nyssaceae), *Magnolia cylindrica* (Magnoliaceae), and *Cyclocarya paliurus* (Juglandaceae), some of which were also distributed at low altitudes. *Cercidiphyllum japonicum* (Cercidiphyllaceae) and *Ginkgo biloba* (Ginkgoaceae) were naturally distributed around this altitude.

Community structure along the altitudinal gradient

Vertical structure of community

The vertical structure of forests presented a pattern from four layers to three layers (Table S1). Forests below 1,300 m a.s.l. could be divided into four layers: tree layer, subtree layer, shrub layer and herb layer. From

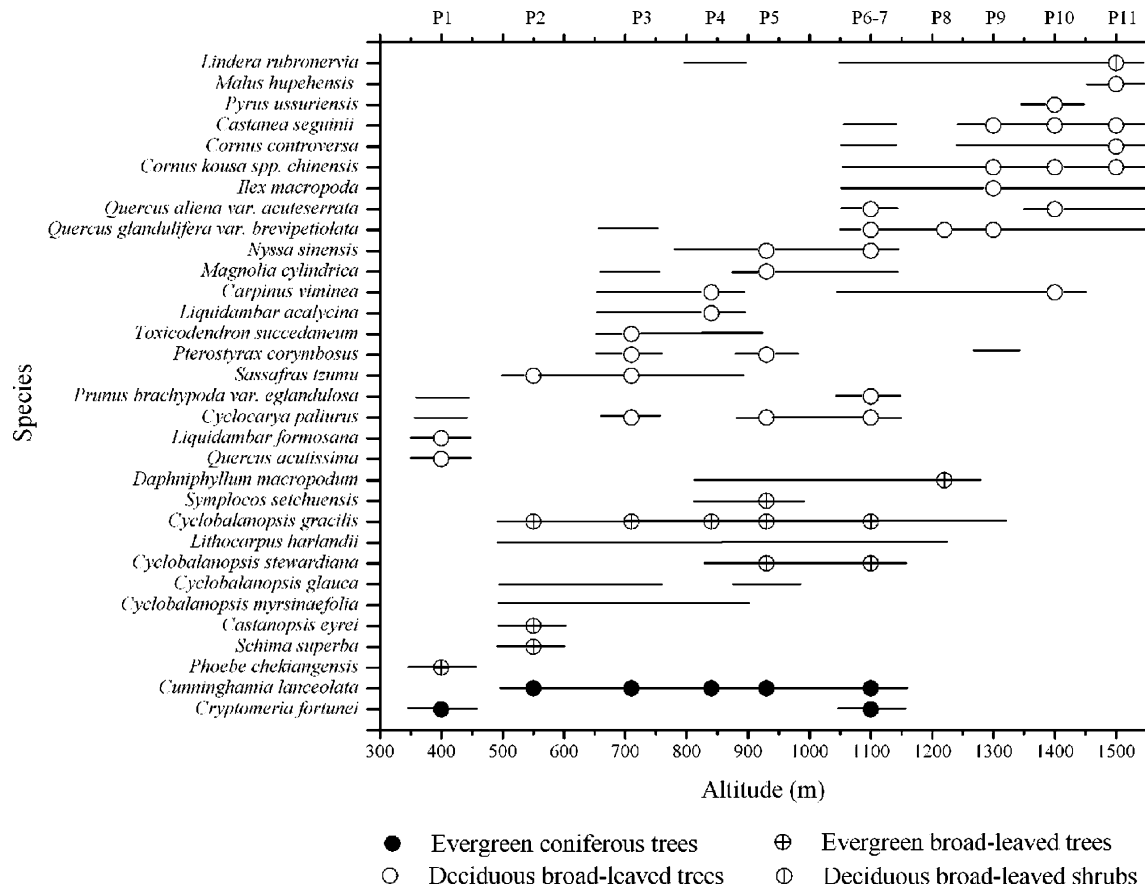


Fig. 3 Altitudinal ranges of dominant species. Circles indicate the plot where the named species is dominant. Dominant species are distinguished by life-form with different circles. P means the plot

1,300 to 1,400 m a.s.l., forests consisted of tree layer, shrub layer, subshrub layer, and herb layer. In plot 11 (1,500 m a.s.l.), the forest had only three layers: the shrub layer, the subshrub layer, and the herb layer.

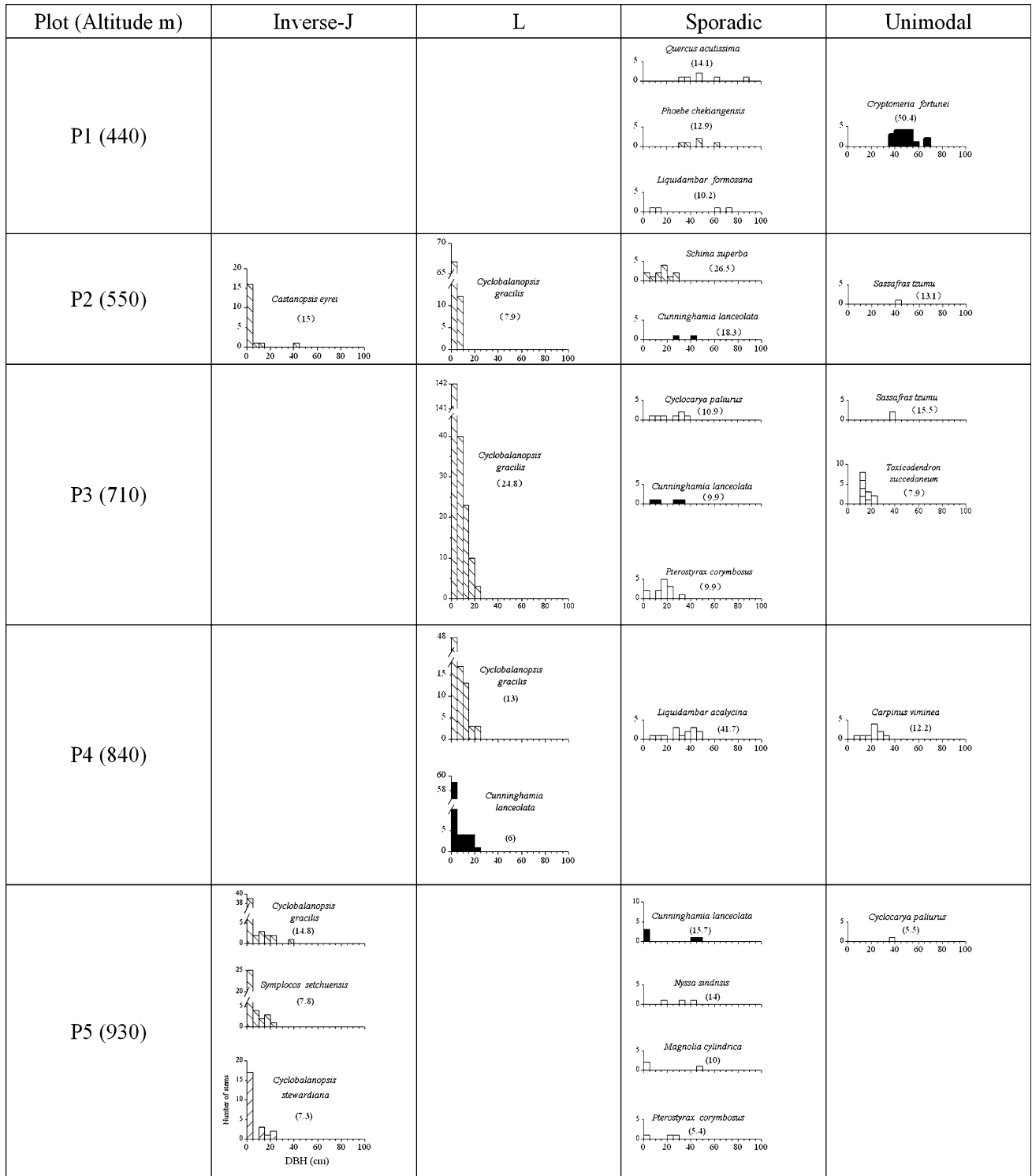
The height class distribution along altitude is indicated in Fig. S2. The maximum tree height showed a unimodal pattern along altitudinal gradients, *C. fortunei* reached 36 m in height, forming the emergent layer in plot 7 (1,100 m a.s.l.). In other plots, the uppermost layers were taken by deciduous tree species. In plot 1 (400 m a.s.l.), evergreen conifers and deciduous trees primarily constituted the tree layer, reaching the height of 24 and 25 m, respectively; only a few evergreen and deciduous broad-leaved species occurred in the shrub layer. In plot 2 (550 m a.s.l.), most of the layers were composed of evergreen broad-leaved species, where the canopy of *S. tzumu* and *Cunninghamia lanceolata* reached 18 m in height and the subcanopy of *Schima superba* reached 14 m in height. In plots 3–5 (710–930 m a.s.l.), deciduous species were mainly distributed in the tree layer, while evergreen broad-leaved species prevailed in the understory. In plot 6 (1,100 m a.s.l.), *Q. glandulifera* var. *brevipetiolata* and *N. sinensis* reached 22 m in height. The forest at this altitude was co-dominated by evergreen and deciduous broad-leaved species

in the understory, even in the *C. fortunei* forest. In plot 8 (1,220 m a.s.l.) *Q. glandulifera* var. *brevipetiolata* towered above evergreen trees reaching a maximum height of 16 m, while *Daphniphyllum macropodum* dominated the subtree layer with a maximum height of 12 m. As altitude increased, evergreen species disappeared, with the exception of *C. gracilis* in the lower tree layer and *Eurya hebeclados* in the shrub layer in plot 9 (1,300 m a.s.l.). Above 1,220 m a.s.l., deciduous species predominated. The maximum tree height decreased from 12 m (plot 9, 1,300 m a.s.l.) to 8 m (plot 11, 1,500 m a.s.l.). Most of the trees were below 5 m in height in plot 11 (1,500 m a.s.l.).

Regenerative pattern of dominant species

DBH class-frequency distributions of dominant species are shown in Fig. 4. In plot 1, at 400 m a.s.l., planted *C. fortunei* showed a unimodal size distribution. The other three co-dominants were represented sporadically in middle or large DBH size classes.

At 550–1,250 m a.s.l. (plots 2–8), most of the evergreen species occurred by the inverse-J type or L-type distribution, with abundant small trees such as



Evergreen coniferous trees
 Deciduous broad-leaved trees
 Evergreen broad-leaved trees
 Deciduous broad-leaved shrubs

Fig. 4 DBH class-frequency distribution of dominant species in each plot. There were four types of the frequency distribution pattern of DBH size class of populations: the inverse-J type, L-
C. gracilis, *Symplocos setchuensis*, and *C. stewardiana*. The population structure of *C. gracilis* showed the L-type at 550–850 m a.s.l. (plots 2–4), and the inverse-J type at

type, sporadic type, and unimodal type. Species are distinguished by life-form with different columns. *DBH* means the diameter at breast height. *P* means the plot

950–1,250 m a.s.l. (plots 5–8). This trend was due to past logging of timbers through clear-cuts or selective felling, which caused the absence of large size classes of

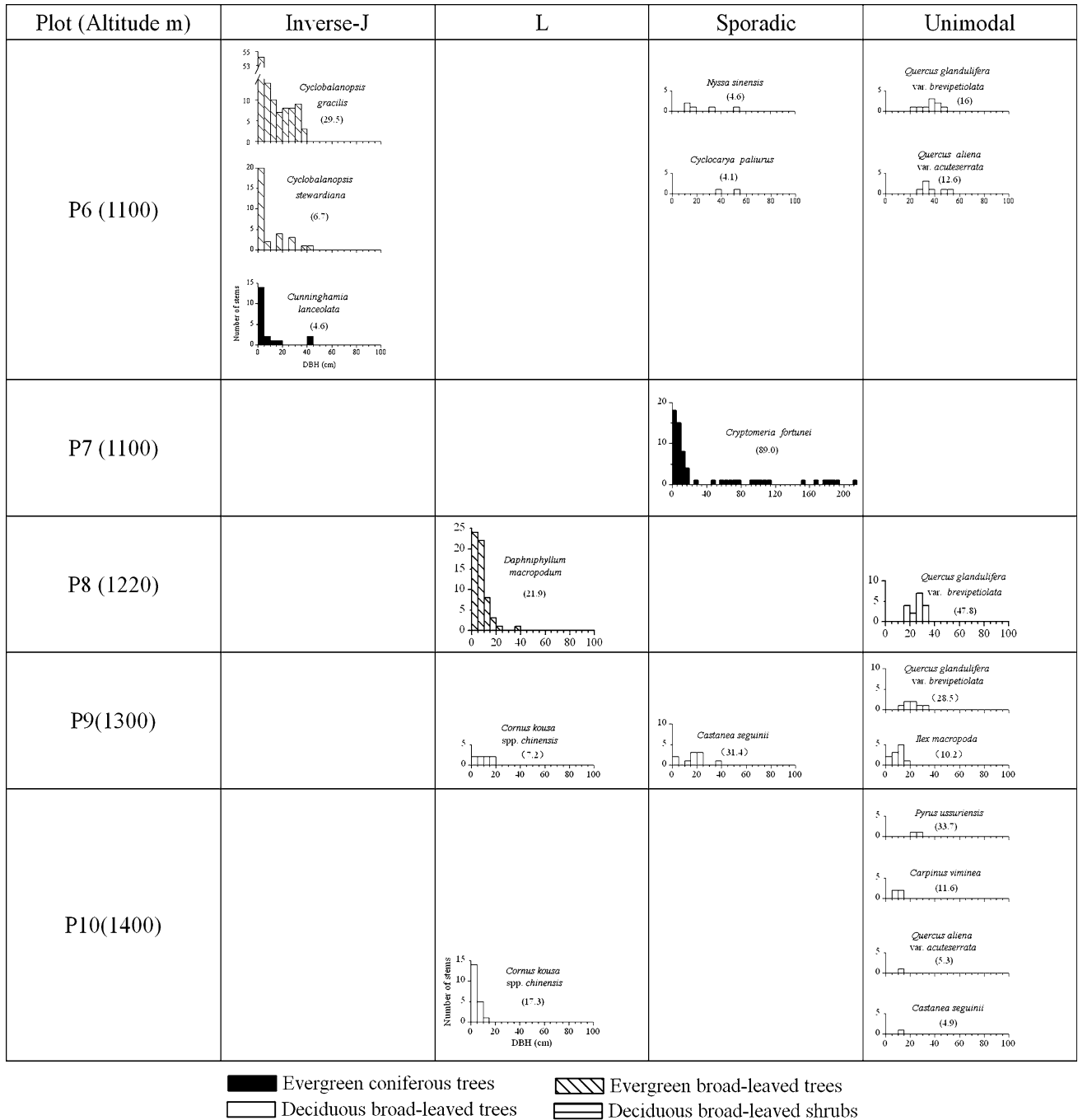


Fig. 4 continued

C. gracilis at low altitudes. *C. gracilis* developed well at higher altitudes, where human disturbances are lesser common.

C. lanceolata was an important component of subtropical evergreen broad-leaved forest and was a principal source of livelihood to the mountain people of the Mt. Tianmu before the establishment of the Nature Reserve. Selective extract or lop this tree for fuel wood, timber and litter has resulted in a complex size-distribution pattern of *C. lanceolata* across altitudinal gradients with many individuals sprouted from

the cut stems. *C. lanceolata* shifted from the sporadic type with few middle and large individuals at 550 m a.s.l. (plot 2), to the L-type at 840 m a.s.l. (plot 4), to the sporadic type with small and large individuals at 930 m a.s.l. (plot 5), to the inverse-J type at 1,100 m a.s.l. (plot 6).

However, most of the deciduous broad-leaved species represented the sporadic or unimodal distribution type. *L. acalycina* at 840 m a.s.l. (plot 4), and some Tertiary relict plants at 710–1,100 m a.s.l. (plots 3, 5, 6) were of the sporadic type. *S. tzumu*, *T. succedaneum*, *Carpinus*

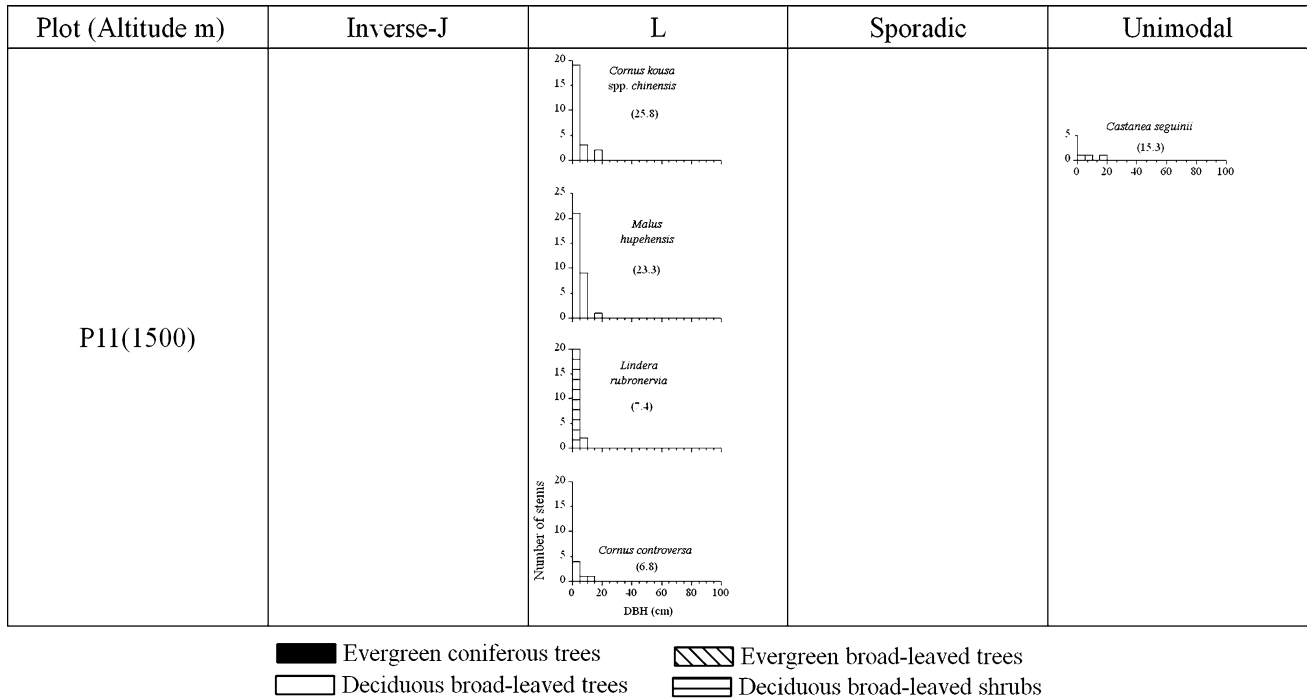


Fig. 4 continued

viminea, *Q. glandulifera* var. *brevipetiolata*, *Q. aliena* var. *acuteserrata*, and *Pyrus ussuriensis* presented emergent in the large size classes without saplings. Above 1,250 m a.s.l., *C. kousa* ssp. *chinensis*, *M. hupehensis*, *L. rubronervia* and *C. controversa* were represented by the L distribution type.

C. fortunei, the single dominant in plot 7 (1,100 m a.s.l.) was represented sporadically in middle or large DBH size classes with three distinct peaks of 0–30, 45–115, and 150–215 cm DBH.

Discussion

Deduction of potential climax vegetation at low altitudes under human disturbance and division of altitudinal vegetation zones

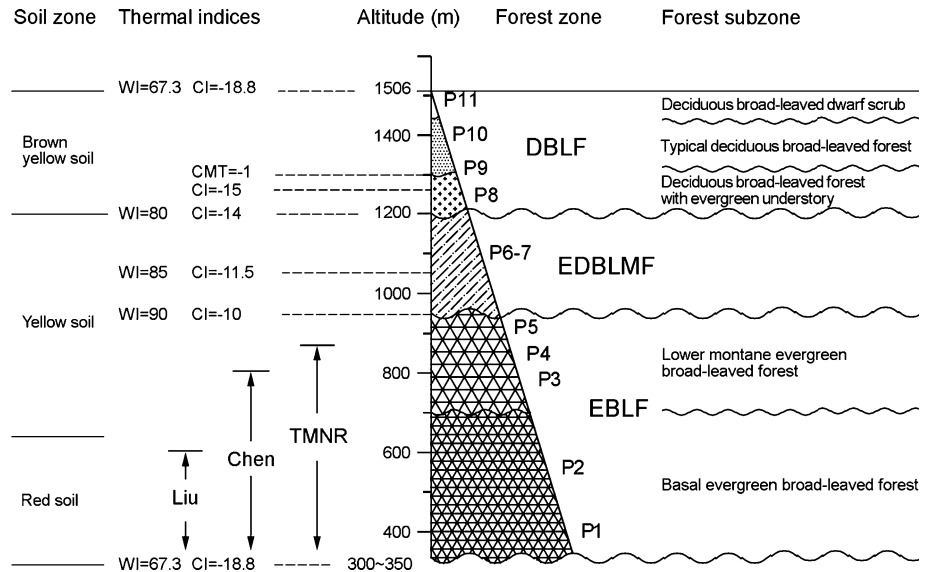
In plot 1 (400 m a.s.l.), projections based on the vegetation patterns we observed indicated that *P. chekiangensis* and *L. formosana*, the typical species of ravine forest (Lin et al. 2007), would develop at low altitudes, while the *C. fortunei* plantation would disappear without the introduction of young individuals. In addition, the pioneer *Q. acutissima* would regenerate only with the appearance of a large bare area. Thus, in the absence of disturbance, this forest would likely develop into the topographic climax community typical of foothill ravines.

Vegetation at 550–950 m a.s.l. was composed of evergreen broad-leaved forest with reduced dominance

of evergreen broad-leaved species and abundant invading deciduous broad-leaved species. The regeneration cycle of the pioneer or seral deciduous broad-leaved species depended on the appearance of gaps formed by storms, soil erosion, and other unpredictable natural forces. The Tertiary relict plants dominating some patches at middle altitudes seem to require unstable habitats where they escape competition from evergreen broad-leaved trees, such as the steep sides of deep ravines (Tang and Ohsawa 1997; Calleja et al. 2009). On the other hand, evergreen broad-leaved species could regenerate even in the closed canopy forest, as they dominate the subtree and shrub layers with abundant saplings. Therefore, evergreen broad-leaved species would dominate at low altitudes as time goes by.

The evergreen broad-leaved forest at 550–950 m a.s.l. can be divided into two subforests according to the dominant species. At 550–700 m a.s.l., the main dominant *S. superba* has characteristics between a pioneer and climax species (Da and Ohsawa 1992; Song and Wang 1995), as represented by its sporadic size distribution. It is shade-tolerant as a seedling, but less shade-tolerant as a medium or large individual, often occurring in large gaps or at the forest edge (Da et al. 2004). Its regeneration was opportunistic and fluctuating. In contrast, *C. eyrei*, one of the representative species of subtropical evergreen broad-leaved forests in China (Xu et al. 2005; Editorial Committee for Vegetation of Zhejiang 1993), would regenerate in a more stable pattern. Therefore, *C. eyrei* forest would be the climax vegetation at the base of the mountain. From 700 to

Fig. 5 Patterns of vegetation zonation, thermal indices and soil zonation (Xia 2004) on Mt. Tianmu along the altitudinal gradient. *WI* means the warmth index ($^{\circ}\text{C}$ months); *CI* means the coldness index ($^{\circ}\text{C}$ months); *CMT* means the coldest mean monthly temperature ($^{\circ}\text{C}$); *EBLF* means evergreen broad-leaved forest; *EDBLMF* means evergreen and deciduous broad-leaved mixed forest; *DBLF* means deciduous broad-leaved forest; Liu, Chen and TMNR mean ranges of evergreen broad-leaved forest according to Liu (1991), Chen (1992) and Tianmu Mountain Nature Reserve (1992), respectively; *P* means the plot



930 m a.s.l., the lower montane climax species *C. gracilis* (Chen et al. 1997) prevailed, which displayed an inverse-J or L-type size distribution patterns. *C. gracilis* forest would be the potential climax vegetation at this altitude.

Above 1,000 m a.s.l., much of the forest was primary vegetation and human disturbance was minimal. Forest at 1,100 m a.s.l. had the physiognomy of evergreen and deciduous broad-leaved mixed forest with patches of coniferous forests. Of the seven co-dominants in plot 6 (1,100 m a.s.l.), *Q. glandulifera* var. *brevipetiolata* and *Q. aliena* var. *acuteserrata* are the main components at the middle altitudes of subtropical montane forest (Editorial Committee for Vegetation of Zhejiang 1993; Wu 2000). Although they displayed the unimodal size distribution type and were shade-intolerant, the tall stature and the long life spans of these species may enable them to emerge under suitable conditions. *Q. aliena* var. *acuteserrata* could regenerate via the large number of nuts and with the appearance of occasional canopy openings (Liu et al. 2000).

C. fortunei forest is one of the unique vegetations on Mt. Tianmu, distributed 350–1,100 m a.s.l. It grows well at middle altitude, the cloudy belt with the ample precipitation and many complex landscape structures (Zhou et al. 1992). The shade-intolerant nature made its regeneration only occurred in special habitats, such as fallen woods, logging stakes, gaps, cliffs (Xia et al. 2004), but the relative large size and long life spans ensured its dominant in unstable habitats at middle altitudes. The forest type should be considered as the remnant forest patch of the mixed mesophytic forest (Wang 1961), and the topographic climax at this area.

Species richness was highest at 1,100 m a.s.l., possibly due to the occurrence of habitats suitable for Tertiary relic plants stemming from the glacial period (Cao et al. 2008), the higher heterogeneity of topography and community structure at this altitude, the edge effect of

the mixed forest (Zhao et al. 2005), the perfect hydrothermal conditions (Minchin 1989; Wang 2002; Wang et al. 2004), and the highest precipitation (Kitayama 1992; Md Nor 2001; Jiang and Zhang 1992) at the middle altitudes.

Above 1,200 m a.s.l., vegetation appeared as deciduous forest, which can be divided into three subforests according to the community structures. Forests at 1,200–1,300 m a.s.l. (plot 8) showed a physiognomy of deciduous broad-leaved forest with *Q. glandulifera* var. *brevipetiolata* occupying the tree layer and evergreen *D. macropodum* dominating in the subtree layer. Above 1,300 m a.s.l., deciduous broad-leaved species predominated. Deciduous broad-leaved forest at 1,300–1,450 m a.s.l. (plots 9, 10) was co-dominated by *C. seguinii*, *Q. glandulifera* var. *brevipetiolata*, *C. kousa* ssp. *Chinensi*, and *P. ussuriensis*. Due to the effects of strong winds, the physiognomy of vegetation in plot 11 (1,500 m a.s.l.) was a deciduous broad-leaved dwarf scrub, mainly composed of *C. kousa* ssp. *chinensis* and *M. hupehensis*.

Based on the potential climax vegetation deduced from the regenerative patterns of the dominant species, combined with the floristic composition and community structure along an altitudinal gradient, the vertical vegetation of Mt. Tianmu was divided into three zones (Fig. 5): (1) evergreen broad-leaved forest zone at (300–350) to 950 m a.s.l., (plots 1–5), including the basal evergreen broad-leaved forest subzone at (300–350) to 700 m a.s.l. (plots 1–2) and the lower montane evergreen broad-leaved forest subzone at 700–950 m a.s.l. (plots 3–5), (2) evergreen and deciduous broad-leaved mixed forest zone at 950 to (1,200–1,250) m a.s.l. (plots 6, 7), and (3) deciduous broad-leaved forest zone at (1,200–1,250) to 1506 m a.s.l. (plots 8–11), composed of the deciduous broad-leaved forest subzone with evergreen understory at (1,200–1,250) to 1,300 m a.s.l. (plot 8), the typical deciduous broad-leaved forest subzone at

1,300–1,450 m a.s.l. (plots 9, 10), and the dwarf scrub subzone at 1,450–1,506 m a.s.l. (plot 11).

There are many different views concerning the altitudinal vegetation zonation of the southern slope of Mt. Tianmu. The main dispute involves the upper limit of the evergreen broad-leaved forest zone. Chen (1992) considered the upper distributive limits of the present and the successive climax vegetation of the evergreen broad-leaved forests to be 660 and 796 m a.s.l., respectively. Liu (1991) claimed that the evergreen forests are distributed below 600 m a.s.l. According to the Comprehensive investigation team of Tianmu Mountain Nature Reserve (1992), the evergreen broad-leaved forests occur below 870 m a.s.l. Feng (1956) suggested that the evergreen and deciduous broad-leaved mixed forests occur below 1,000 m a.s.l. The chief reason for the disagreement is that abundant deciduous species coexisted with evergreen broad-leaved species in the secondary forest at low altitudes (below around 1,000 m a.s.l.) due to a long history of human activity. When the climax forests were destroyed, pioneer or seral species, which can be the climax species of higher altitudes, will descend to lower altitudes (Ohsawa 1984). This has resulted in seral vegetation with an obscure zonal sequence on Mt. Tianmu.

The relationship between distribution of vegetation and thermal conditions

Climatic factors are critical to the division of vegetation, especially thermal factors that limit for the vegetation distributions such as the WI, CI, and CMT (Kira 1977; Xu 1983; Fang and Yoda 1989; Federici and Pignatti 1991; Nakamura et al. 2007). The relationship between the northern or upward distribution of evergreen broad-leaved forest and the thermal indices has been a topic of much focus (Wolfe 1979; Hattori and Nakanishi 1985; Kira 1991; Ohsawa 1990; Fang and Yoda 1991; Fang et al. 2002). Kira (1991) concluded that the borderline between the deciduous broad-leaved forest and the evergreen

broad-leaved forest corresponds approximately to the WI of 85°C months under a maritime climate in East and Southeast Asia; however, the northward or upward distribution of evergreen broad-leaved forest tends to be limited by the critical CI of –10°C months. Fang et al. (1996) suggested low temperature in winter controls the upper distribution of evergreen broad-leaved forest in the eastern part of the 30°N latitude belt in humid East Asia. In other words, the critical CI values are between –10 and –15°C months. On Mt. Tianmu, the CI of –10°C months corresponded to an elevation of 950 m, and was more effective as an upper limit of evergreen broad-leaved forest than the WI of 85°C months (Fig. 5). The CI of –15°C months occurred at approximately 1,260 m a.s.l. corresponding to the upper limit of evergreen and deciduous broad-leaved mixed forest on Mt. Tianmu.

Ohsawa et al. (1985) concluded that the –1°C isotherm (range –2 to 1°C) coincides closely to the northern or upper limit of evergreen broad-leaved trees in humid East and South Asia. The CMT of –1°C occurred at 1,300 m a.s.l., coinciding with the upper limit of evergreen broad-leaved trees on Mt. Tianmu (Fig. 5). Thus, though the upper limit of evergreen and deciduous broad-leaved mixed forest was at around 1,200–1,250 m a.s.l., *C. gracilis* and *E. hebeclados* could extend up to 1,300 m a.s.l. in the understory of deciduous broad-leaved forest, and some evergreen broad-leaved shrubs were even found up to 1,400 m a.s.l. outside the plots on Mt. Tianmu.

In Japan, the WI of 85°C months, the CI of –10°C months and the CMT of –1°C coincide approximately with the northern or upper limit of evergreen broad-leaved forest in Japan (Kira 1991; Ohsawa 1990). However, the three temperature conditions occurred at different altitudes on Mt. Tianmu. This may be because temperature conditions on Mt. Tianmu are intermediate between tropical and temperate mountains (Ohsawa 1990, 1991); this phenomenon is also found on Mt. Emei in western China (Tang and Ohsawa 1997). In temperate regions, the strong seasonal climate often causes the three temperature conditions to coincide (Ohsawa 1990,

Table 1 Thermal vegetation zones in Japan, China, and Mt. Tianmu

Vegetation type	WI (°C months)	CI (°C months)
Thermal vegetation zones in Japan (Kira 1949, 1976, 1977)		
Boreal coniferous forest	15–45	
Cool-temperate deciduous broad-leaved forest	45–85	
Warm-temperate evergreen broad-leaved forest	85–180	> –10
Subtropical rain forest	180–240	
Latitudinal thermal vegetation zones in China at humid condition (Fang et al. 2002)		
Cool-temperate coniferous forest	< 50	
Temperate mixed coniferous and deciduous forest	50–90	
Warm-temperate deciduous broad-leaved woodland	90–120	< –10
Warm-temperate deciduous and evergreen broad-leaved forest	120–135	> –10
Subtropical evergreen broad-leaved forest	135–240	
Tropical rain forest and monsoon forest	> 240	
Altitudinal thermal vegetation zones on the southern slope of Mt. Tianmu in this study		
Deciduous broad-leaved forest	67.3–80	–18.8 to 14
Deciduous and evergreen broad-leaved forest	80–90	–14 to –10
Evergreen broad-leaved forest	90–120	–10 to –3

WI the warmth index, CI the coldness index

1991). This could explain the existence of a distinctive evergreen and deciduous broad-leaved mixed forest on Mt. Tianmu.

By comparison, the altitudinal thermal vegetation zones on Mt. Tianmu according to the altitudinal vegetation zones in this study were more similar to the thermal vegetation zones in Japan than to the latitudinal thermal vegetation zones in China (Table 1). This is because the distribution of vegetation along horizontal and altitudinal gradients is limited mainly by thermal conditions, as precipitation is plentiful in Japan's oceanic climate (Fang et al. 2002). However, because of the continental climate in many parts of China, limited precipitation causes the corresponding vegetation zone to move southward or downward (Kira 1991). For this reason, the values of critical thermal indices for vegetation zones in China are higher than in Japan or on Mt. Tianmu. Fang (2001) and Fang et al. (2002) suggested the evergreen broad-leaved forest in eastern China does not reach the thermal northern limit due to the deficiency of precipitation. However, the evergreen broad-leaved forest can reach the upper altitudinal limit where there is ample precipitation captured by the mountains in eastern China (Fang and Yoda 1991; Fang 2001).

Comparison of the vertical distribution of conifers along 30°N latitude in humid East Asia

Fang et al. (1996) pointed out that a subalpine conifer forest zone exists in the western part, while there is no conifer forest zone in the eastern part because of the lack of enough high mountains, via studying the vertical vegetation zones on 20 mountains along 30°N latitude in humid East Asia. We considered that the subalpine conifer forests in the west inland were zonal vegetation, conifers at low and middle altitudes in the western and the lower mountains in the eastern part were azonal or transitional species in between warm-temperate/subtropical and cool-temperate zones. They played important roles on vertical vegetation in humid East Asia.

Azonal conifers appeared spanning in several climatic zones as pioneer species and the appearances were controlled not by climatic factors but by disturbances. Most of the azonal conifers were *Pinus* species, such as *Pinus yunnanensis* (600–3,100 m a.s.l.) in the west inland, *Pinus massoniana* (below 800 m a.s.l.) and *Pinus taiwanensis* (above 800 m a.s.l.) in the east coastland (Zheng 1998).

Many species of *Abies*, *Tsuga*, *Cryptomeria*, and *Cunninghamia* appeared as the transitional species coexisting with broad-leaved species. They acted as components of evergreen broad-leaved forests or pioneers of climax in unstable habitats, establishing perfect microhabitat for later evergreen broad-leaved species. The conifers included *Tsuga chinensis* on Mt. Gongga (2,200–2,500 m a.s.l., 29°40'N, 101°50'E, Liu and Qiu 1986), *Tsuga dumosa* on the eastern Himalayas (2,200–3,300 m a.s.l., 27°59'N, 86°55'E, Zheng and Chen 1981) in the west inland; *Tsuga chinensis* var. *tchekiangensis*,

Cephalotaxus fortunei and *Cryptomeria fortunei* on Mt. Tianmu (300–1,100 m a.s.l., Zhou et al. 1992), Huangshan (800–1,600 m a.s.l., 30°08'N, 118°09'E, Hu and Liang 1996) and Jiulongshan (1,000–1,600 m a.s.l., 28°21'N, 118°52'E, Zhang et al. 1996) in the east coastland; *C. lanceolata* in the west inland (below 2,000 m a.s.l.) and east coastland (below 1,000 m a.s.l., Wu 1984); *Tsuga sieboldii*, *Abies firma* and *Cryptomeria japonica* on Yakushima (350–1,701 m a.s.l., 30°27'N, 130°30'E, Izumoto unpublished data) in the east island.

It was interesting to note that *Cryptomeria* forests exist on Mt. Tianmu in the east coastland and Yakushima in the east island. They face each other across the East China Sea. *Cryptomeria* favors warm and humid climate, especially the oceanic or mountain climate (Zheng 1998). It occurred in between vertical warm-temperate/subtropical and cool-temperate zones, but in most of the cases it appeared as the emergent trees of uppermost evergreen broad-leaved forests or in the lowermost zone of the deciduous broad-leaved forest zone.

As the remnant giant conifers, *C. fortunei* and *C. japonica* form the emergent layer towering above evergreen and deciduous broad-leaved canopy on Mt. Tianmu (900–1,100 m a.s.l.) and Yakushima (900–1,701 m a.s.l., Aiba et al. 2007; Izumoto unpublished data), respectively. On Mt. Tianmu, *C. fortunei* grows well at cloudy belt with the most precipitation along altitude (Jiang and Zhang 1992; Xia et al. 2004), and disappears at high altitudes due to limitation of hydrothermal condition, especially the lower temperature and little precipitation in winter. It cannot tolerate the mean temperature of January below 0°C (Zheng 1998). And then deciduous broad-leaved forest zone existed above 1,100 m a.s.l. However, *C. japonica* dominates at higher altitudes (1,240–1,701 m a.s.l.) on Yakushima with an average annual precipitation of 4,000–5,000 mm in oceanic climate. The emergent status of *C. japonica* limited the dominance of deciduous broad-leaved species. Therefore, the deciduous broad-leaved forest is not seen as a forest zone in Yakushima (Izumoto unpublished data). But due to the weak regeneration, the declining *Cryptomeria* forest would be replaced by evergreen or deciduous broad-leaved forest on Mt. Tianmu and Yakushima.

Conclusions

Abundant deciduous species coexist with evergreen broad-leaved species in the secondary forest at low altitudes (below 1,000 m a.s.l.) on Mt. Tianmu due to a long history of human activities. This has resulted in seral vegetation with an obscure zonal sequence on Mt. Tianmu. The potential climax vegetation was deduced from the regeneration patterns of the dominant species combined with the floristic composition and community structure of each altitudinal level, and this information was used to divide the altitudinal vegetation

zones of Mt. Tianmu. The altitudinal vegetation zones classified in this study coincided with thermal conditions. The distribution of vegetation on Mt. Tianmu was limited mainly by thermal conditions without shortage of precipitation. Thus, the altitudinal thermal vegetation zones on Mt. Tianmu were more similar to thermal vegetation zones in Japan's oceanic climate than in China's continental climate.

The vertical distributions and roles of conifers were different between the east and west along 30°N latitude in humid East Asia. *Cryptomeria fortunei* possessed emergent status towering above broad-leaved canopy at middle altitudes as *C. japonica* on Yakushima, but disappeared at high altitudes with the limitation of hydrothermal condition on Mt. Tianmu.

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