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ORIGINAL ARTICLE

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Plant diversity patterns in subtropical evergreen broad-leaved forests of Yunnan and Taiwan

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Abstract The subtropical evergreen broad-leaved forests of Yunnan and Taiwan were compared along environmental and successional gradients with the aim of identifying important taxon and species diversity as well as the drivers of mountain biodiversity patterns. A detrended correspondence analysis of an exhaustive set of data collected from 105 and 223 plots for Yunnan and Taiwan, respectively, was applied to classify natural mature forest types. Additional data from 72 and 68 plots for Yunnan and Taiwan, respectively, were used for analyses of secondary succession. The floristic richness and diversity index were calculated for each type of forest. In Yunnan, the monsoon forests in mesic-humid sites had more taxa and tended to show higher species diversity than the other two forest types. In Taiwan, species diversity values were significantly higher in the *Machilus–Castanopsis* zone in the middle altitudes (500–1500 m) than for the other three forest zones. For both Yunnan and Taiwan, the forests at the middle successional stage showed significantly higher species diversity than those at the early successional stage. Differences in diversity between the middle and late stages were not significant. These findings highlight the high species diversity of the natural mature evergreen broad-leaved forests of both Yunnan and Taiwan. In the secondary forests, as succession proceeds, species diversity comes to resemble that of the natural mature forests. In both ecosystems, the drivers of species diversity patterns are moisture, altitude, and succession/disturbance.

Keywords Diversity · Environmental gradient · Floristic richness · Forest types/zones · Successional gradient

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Introduction

Subtropical ecosystems of evergreen broad-leaved forests contribute to biodiversity and to sustainable development. The natural subtropical evergreen broad-leaved (lucidophyllous) forest dominated by the genera *Castanopsis*, *Lithocarpus*, *Cyclobalanopsis* (Fagaceae), *Machilus* (Lauraceae), *Schima* (Theaceae), *Distylium* (Hamamelidaceae), *Magnolia*, and *Michelia* (Magnoliaceae) is almost exclusively confined to eastern Asia, including southern, southwestern, and southeastern mainland China, and Taiwan, as well as southwestern Japan and a number of tropical mountain regions of Vietnam, Laos, Thailand, Myanmar, India, Bhutan, and Nepal (Kira 1991; Ohsawa 1993; Tagawa 1995). The trees of these forests are distinguished from those of evergreen sclerophyllous forests by their leaf morphology, physiognomy, and structure (Ovington 1983; Satoo 1983; Hattori 1985; Wu et al. 1987). Primary evergreen broad-leaved forests once covered most of those areas, but these are now greatly diminished as a result of human activity. In these regions of Yunnan and Taiwan, extensive secondary forests have recently developed on land previously used for firewood or agriculture in the 19th and earlier 20th centuries. Remnants of the natural subtropical evergreen broad-leaved forests are only found in remote isolated areas, on steep slopes, around temples in Yunnan, and in nearly inaccessible or protected areas in forest reserves as well as natural parks of Taiwan. Yunnan and Taiwan have the most diversified subtropical evergreen broad-leaved forests of eastern Asia (Kudo and Sasaki 1931; Liu 1968; Su 1984; Wu et al. 1987; Hsieh et al. 1997; Tang and Ohsawa 2009; Tang 2010). Taiwan, located off the southeast coast of mainland China, is traversed by the Tropic of Cancer. High mountains divide the east from the west of the island. A landbridge connected southeastern China, Taiwan, and the Ryukyu Islands during the early Pleistocene about 1.5 million years (My) ago, and it may have lasted into the middle Pleistocene (about 1 My; Kizaki and Oshiro 1977). Species from southwestern China may have migrated through the Yunnan–Guizhou Plateaus to regions further east eventually reaching Taiwan by the landbridge (Huang 2011), as evidenced by the island flora which includes elements from the Sino-Himalaya, Sino-Japanese, Japan, and Philippines regions. In terms of phytogeography, the subtropical vegetation of both Yunnan and Taiwan is located around the boundary between the extensive Holarctic and Paleotropical floristic kingdoms, belonging to the east Asiatic region (de Laubenfels 1975; Takhtajan 1986). The forests of both Yunnan and Taiwan include elements of the two floristic kingdoms intermingled, with many species closely related to each other (Wu 1980; Wu and Wu 1996; Hsieh 2002). The subtropical evergreen broad-leaved forest zone extends roughly from 21° to 28°N in Yunnan and from 21° to 25° N in Taiwan, marking the northern limit of the tropics and the ecotone between the tropical and temperate zones. A study of the evergreen broad-leaved forests of Yunnan and Taiwan can broaden our understanding of the global pattern of vegetation. The widespread loss and fragmentation of natural mature evergreen broad-leaved forests have motivated studies on the regeneration dynamics, secondary succession, and soil seed bank of the evergreen broad-leaved forests in Yunnan (Tang et al. 2007, 2010; Tang and Ohsawa 2009; Li et al. 2010; Tang 2010) and on the floristic composition, structure, and dynamics of their counterparts in Taiwan (e.g. Su 1984; Hsieh et al. 1997, 1998; Fan et al. 2005; Chao et al. 2010; Chang et al. 2010; Song et al. 2010). However, there have been no diversity studies comparing the evergreen broad-leaved forests of Yunnan and Taiwan.

Comparative studies of ecosystem types can provide insights into the relative importance of processes that influence diversity (Tilman and Pacala 1993). Biodiversity is often expressed on a variety of spatial scales, including patch, stand, landscape, and from local to global (Crow 1990; Petraitis et al. 1989; Oliver and Larson 1990; Auclair and Goff 1971), or it may be seen through changing competitive interactions over time (Peet and Christensen 1988; Oliver and Larson 1990). Successful forest conservation and management should be based on an understanding of natural patterns of diversity and the ecological processes that influence them (Roberts and Gilliam 1995). The aim of our study was to compare plant diversity of the evergreen broad-leaved forests of Yunnan and Taiwan along environmental and successional gradients and to identify the drivers of mountain biodiversity patterns. We address the following questions: (1) what are the similarities or differences in the floristic composition of these geographical regions? (2) what are the plant diversity patterns along the environmental gradients? (3) what are the plant diversity patterns during succession?

Methods

Location, climate, vegetation

Yunnan

Yunnan is located in southwestern China (21°8′32″–29°15′8″N, 97°31′39″–106°11′47″E). It is a highland province with a terraced topography stretching along one of the greatest altitudinal gradients on earth from the northwest (6740 m a.s.l.) to the southeast (76 m a.s.l.). Set in the foothills of the Himalayas and Tibet, Yunnan's climate ranges from the icy highland climate of the northwestern frontier to the tropical lowland climate of the area bordering Myanmar and extending south and east toward Laos and Vietnam. Most of the province falls into latitudes classified as middle subtropics (25°–29°15′) and southern subtropics (22°–25°) (Hou 1983). The climate throughout the subtropical zone is monsoonal, with rainy summers. The subtropical evergreen broad-leaved forests (henceforth EBLFs) are found at altitudes ranging from 1100 to 2900 m a.s.l. and are divided into five subclasses: mid-montane moist, monsoon, semi-humid, montane mossy, montane mossy scrub (Wu et al. 1987). The last two have formed only in very specific topographical habitats. In addition, sclerophyllous evergreen *Quercus* (subgenus *Quercus*) forests thrive at high altitudes with a dry climate in parts of northwestern Yunnan and are similar to the sclerophyllous forests of the areas of Mediterranean climate (Wu et al. 1987; Tang 2006). In this paper, we only deal with the first three types as representative of the typical subtropical EBLFs of Yunnan. The semi-humid EBLF is distributed at altitudes of approximately 1500–2500 m a.s.l. with annual rainfall of approximately 900–1200 mm in central Yunnan. The monsoon EBLF is distributed at altitudes ranging from approximately 800 to 2000 m a.s.l. with annual precipitation of approximately 1100–2500 mm in southeastern, southern, and southwestern Yunnan. The mid-montane moist EBLF is located at altitudes of approximately 2200–2900 m a.s.l. on mountain systems, with annual precipitation of 1700–3700 mm. The climate of the study sites of Mt. Huafu, Qiongzhusi, Xishan, and Luquan in central Yunnan can be classified as subtropical semi-humid seasonal, with an annual rainfall of approximately 1100–1250 mm and a markedly dry season from

November to May. The climate of the study sites in Fadou and Xiaoqiaogou, Xichou of Wenshan, southeastern Yunnan, and Guanping, Nangongshan, Puwen of Xishuangbanna, southern Yunnan can be classified as subtropical monsoonal, with an annual rainfall of approximately 1250–2500 mm. Wenshan is characterized by a limestone landscape, but the study plots in Xiaoqiaogou Reserve are not in the areas with limestone outcrops; these habitats have soil depths of >1 m. Atmospheric moisture is 86 % throughout the year. The climate of the study sites at altitudes of 2250–2755 m a.s.l. on Ailao Mountains and at 1900–2400 m a.s.l. on Gaoligong Mountains can be classified as subtropical mid-montane moist seasonal, with an annual rainfall of approximately 1900–3700 mm (YMB 1995–2005). In our study, locations at altitudes of 1450–2000 m a.s.l. on the eastern slopes of Ailao Mountains were classified as the monsoon EBLF, and those at altitudes of 2000–2200 m a.s.l. as semi-humid EBLF.

Taiwan

Taiwan (21°55′–25°20′N, 119°30′–122°00′E) is situated between the southernmost part (Ryukyu Islands) of the Japanese Archipelago and the Asian continent and runs in a north–south direction east of mainland China, north of the Philippines. Taiwan is dominated by forested mountains, with 30 % of its area strongly undulating between 1000–3000 m a.s.l. More than 200 peaks are higher than 3000 m; all of these are located within the Central Ridge. This lofty range runs basically along the north–south axis of the island (Fig. 1).

Taiwan has a distinctive oceanic subtropical climate (Hsieh et al. 1997). The annual rainfall ranges from 1000 to >4500 mm. With respect to the evergreen broad-leaved forest zone, annual precipitation is approximately 1800–2500 mm at altitudes of <500 m a.s.l., 2350–3000 mm at altitudes of 500–1500 m a.s.l., and approximately 2400–2900 mm at altitudes of 1500–2500 m a.s.l. Mean monthly temperatures in the lowlands range from 15 to 28 °C. Typhoons are not infrequent during the summer and early autumn, but have less impact in western Taiwan, which is sheltered by the Central Ridge. The climate ranges from subtropical in the lowlands to alpine at the highest elevations.

The EBLFs of Taiwan cover a wide altitudinal range from sea level to 2500 m a.s.l. Su (1984) classified the evergreen broad-leaved forests into four altitudinal vegetation zones: *Ficus–Machilus* zone (<500 m a.s.l.), *Machilus–Castanopsis* zone (500–1500 m a.s.l.), lower *Quercus* zone (1500–2000 m a.s.l.), and upper *Quercus* zone (2000–2500 m a.s.l.). Most of the lowland forests have been cleared for agriculture and industry, with only a few modified remnants remaining.

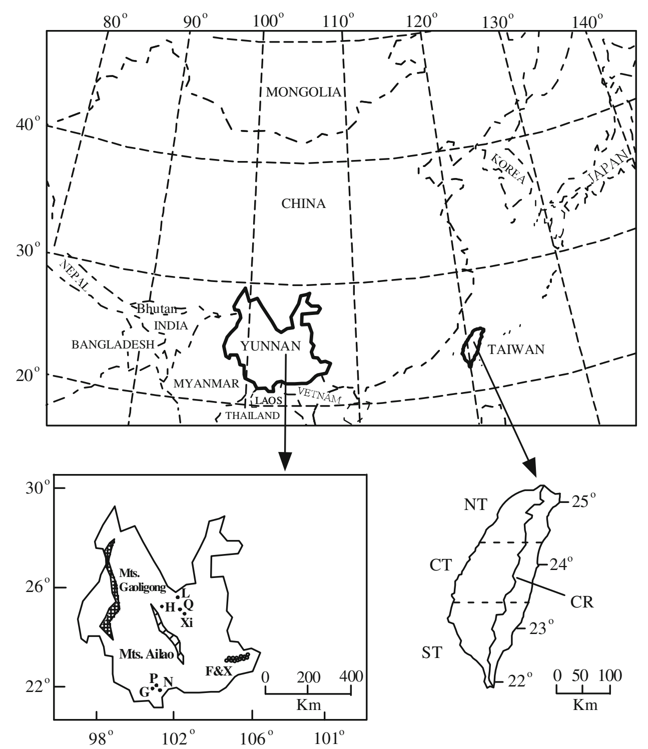

Fig. 1 Map showing location of study sites. *L* Luquan, *Xi* Xishan, *Q* Qiongzhusi, *H* Mt. Fuahu, *F&X* Fadou and Xiaoqiaogou, *G* Guanping, *N* Nangongshan, *P* Puwen. *ST* southern Taiwan, *CT* central Taiwan, *NT* northern Taiwan, *CR* Central Ridge

Data collection

In Yunnan, we selected 105 plots (20 × 20 m each) for sampling the natural mature EBLFs that have been free of major disturbance during the past 60 years as representative of the geographic breadth of the whole province. The study plots selected were on Mt. Huafu (25°24′09″N, 101°28′18″E; 2450 m a.s.l.) at Chuxiong; Luquan, Xishan, and Qiongzhusi (24°57′–25°45′N, 102°37′–102°23′E; 2070–2580 m a.s.l.) in the Kunming area, central Yunnan; Xiaoqiaogou Reserve, including Fadou and Xiaoqiaogou (23°23′–23°25′N, 104°25′–105°57′E; 1400–1700 m a.s.l.) in Xichou; Wenshan, southeastern Yunnan, and Guanping, Nangongshan, Puwen (21°37′–22°30′N, 100°54′–101°26′E; 845–1980 m a.s.l.) in Xishuangbanna, southern Yunnan; Gaoligong Mountains (24°49′45″–27°45′55″N, 98°46′19″–98°36′08″E; 1900–2400 m a.s.l.); the Ailao Mountains (24°05′–25°03′N, 101°01′–102°42′E; 1400–2755 m a.s.l.) (Fig. 1). We also selected plots (20 × 20 m each) at Luquan, Qiongzhusi, Xishan in the Kunming area, Xiaoqiaogou of Wenshan, and the eastern slope of Ailao Mountains to represent various secondary forests at the early (younger secondary forests, 23 plots), middle (older secondary forests, 26 plots), and late (natural mature forests, 23 plots) successional stages of the EBLFs of Yunnan. We defined secondary forests as those once cleared for agricultural or other purposes and later abandoned, or those remaining from the earlier coppice system. We did not consider plantations. In all study plots we recorded all woody species and measured the diameter at breast height (DBH; 1.3 m) of all tree trunks and sprouting stems, as well as the height of all stems. The seedlings and saplings (height < 1.3 m) of woody species were counted and their height measured.

In Taiwan, based on the forest structure, species composition, and information on forest management from local forestry stations, we selected data from the dataset of the National Vegetation Diversity Inventory (NVDI) and Mapping Project (Chiou et al. 2009) on 223 plots (20 × 20 m each) representing the geographic breadth of this island. These plots had been free of major disturbance during the past 60 years and were taken as representative of the natural mature EBLFs of Taiwan. We also selected plots (20 × 20 m each) in the northern and southern Central Ridge, and the Techi Reservoir area of central Taiwan from the dataset of the NVDI to represent the secondary plant communities at early (younger secondary forests, 22 plots), middle (older secondary forests, 32 plots), and late (natural mature forests, 14 plots) successional stages of the EBLFs of the island.

Data analysis

The relative basal area (RBA) at 1.3 m height of each species (DBH ≥1 cm) in each plot on Yunnan and Taiwan was used to delineate the forests according to an ordination method, detrended correspondence analysis (DCA). The PCORD program (McCune and Mefford 1999) was used to perform the analysis. We pooled data on the plots in each forest type/zone to calculate the RBA for each species. Species with an RBA of ≥1.5 % in each forest type were classified as major tree species. The altitudinal forest zones of Taiwan were named using the terminology of Su (1984). In this study, *Quercus* L. subgen. *Cyclobalanopsis* (Oerst.) C. K. Schneid. is treated as an independent genus, *Cyclobalanopsis*, although in his paper on altitudinal forest zones of Taiwan Su (1984) refers to it as *Quercus*. Also, we followed the dataset of the NVDI, and used the genera *Pasania* and *Lithocarpus* separately for Taiwan.

We applied Simpson's diversity index: $D = 1 - \sum p_I^2$ (Lande 1996), where p_I is the proportion of the number of Ith species to total number of individuals. Sørensen's similarity index (beta diversity) at a taxon level was used to compare the evergreen broad-leaved forest of Yunnan as a whole to that of Taiwan: $\beta = 2C/(S_1 + S_2)$ where S_1 = the total number of a taxon recorded in the first forest, S_2 = the total number of a taxon recorded in the second forest, and C = the number of a taxon common to both forests (Sørensen 1948). Plot size was constant across all samples. Differences in species richness and Simpson's diversity index among different forests were analyzed by the non-parametric Kruskal–Wallis all-pairwise comparisons test, using Analyse-it software (Analyse-it Software, Ltd., UK).

Results

Forest types/zones

The ordination of the 105 plots of Yunnan for the first two axes of the DCA is shown in Fig. 2a. Along Axis 2 (with an eigenvalue of 0.521) from the low side in the vertical direction to the upper side, three forest types are distinctive with increasing moisture: the semi-humid EBLF (38 plots), the monsoon EBLF (38 plots) and the mid-montane moist EBLF (29 plots). Axis 1 may show a gradient of topography or soil properties. The major tree species (RBA ≥1.5 %) in each of the three forest types are shown in Table 1. In terms of RBA, the semi-humid EBLF was dominated by tree species of *Cyclobalanopsis*

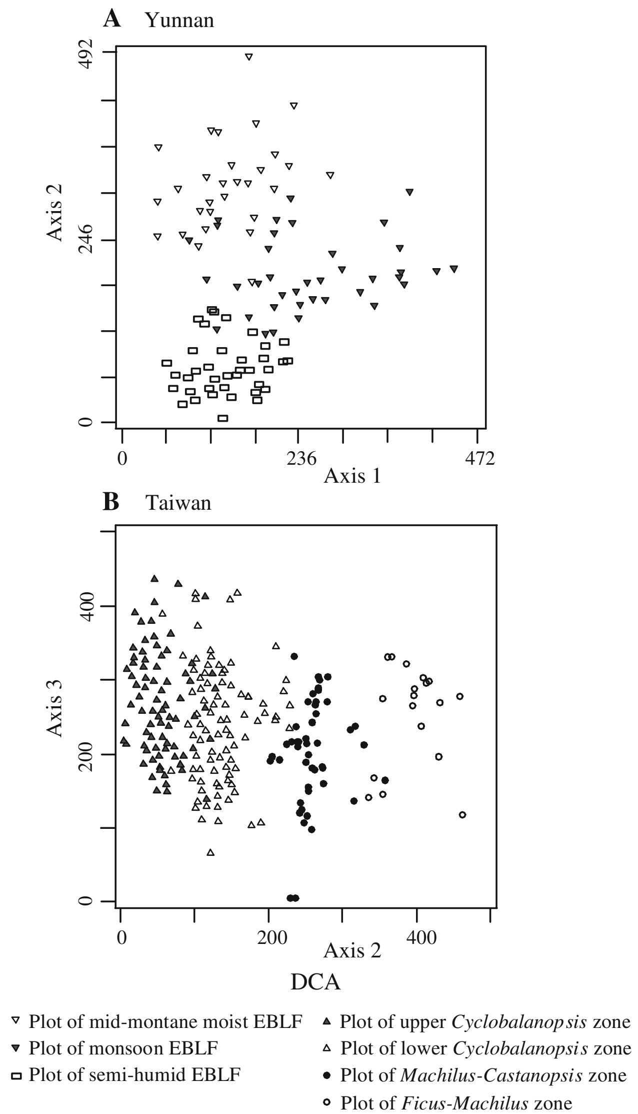

Fig. 2 Ordination of 105 plots along the first two detrended correspondence analysis (DCA) axes for Yunnan (**a**) and of 223 plots along the second and third DCA axes for Taiwan (**b**). *ELBF* Evergreen broad-leaved forest

Table 1 Major tree species (RBA ≥1.5 %) in each forest type of Yunnan

Forest types	Relative basal area (%)		
Species	SH	MS	MM
Castanopsis orthacantha	28.05		
Cyclobalanopsis glaucoides	23.67		
Castanopsis delavayi	14.48		
Cyclobalanopsis delavayi	10.15		
Schima argentea	3.48		
Castanopsis hystrix	3.26	8.56	
Manglietia fordiana	2.29		
Neolitsea homilantha	2.17		
Photinia prionophylla	2.15		
Schima wallichii	2.08	4.18	
Castanopsis calathiformis	1.86	10.17	
Olea yunnanensis	1.75		
Lithocarpus dealbatus	1.54	5.13	
Lithocarpus variolosus	1.51		4.83
Machilus gamblei		3.82	
Michelia coriacea		3.64	
Castanopsis rufoto		2.94	
Castanopsis echinocarpa		2.51	3.05
Castanopsis fabri		2.48	2.32
Lindera thomsonii		2.32	
Machilus longipedicellata		2.23	1.84
Sloanea sinensis		2.16	
Cyclobalanopsis chevalieri		1.89	
Lithocarpus truncatus		1.53	
Lithocarpus hancei			8.59
Lithocarpus pachyphyllus			5.72
Cyclobalanopsis lamellosa			5.40
Castanopsis wattii			5.03
Lithocarpus xylocarpus			4.90
Manglietia insignis			3.08
Michelia floribunda			3.11
Castanopsis remotidenticulata			2.84
Machilus viridis			2.27
Hartia sinensis			2.12
Castanopsis fleuryi			2.09
Schima khasiana			2.05
Cyclobalanopsis myrsinifolia			1.96
Alcimandra cathcartii			1.73
Lithocarpus craibianus			1.68

RBA Relative basal area, *ELBF* Evergreen broad-leaved forest, *SH* Semi-humid EBLF, *MS* monsoon EBLF, *MM* mid-montane moist EBLF, *ELBF* evergreen broad-leaved forests

Table 2 Major tree species (RBA ≥1.5 %) in each altitudinal forest zone of Taiwan

Altitudinal forest zone	Relative basal area (%)			
Species	FM	MCa	LCy	UCy
Machilus japonica var. *kusanoi*	21.13	1.72		
Ficus irisana	15.62			
Bischofia javanica	14.74			
Ficus benjamina	13.08			
Ficus microcarpa	7.91			
Neolitsea konishii	4.37			
Schefflera octophylla	3.10	2.13		
Ficus nervosa	1.88			
Ficus virgata	1.51			
Castanopsis cuspidata var. *carlesii*		8.14	12.04	26.13
Cyclobalanopsis longinux		7.42	10.61	2.90
Beilschmiedia erythrophloia		6.87	3.49	
Quercus variabilis		5.99		
Schima superba		4.94	7.92	5.52
Machilus japonica		3.53	6.18	
Machilus thunbergii		3.38	6.78	2.91
Machilus konishii		3.00		
Castanopsis fabri		2.71		
Pasania shinsuiensis		2.36		
Litsea acuminata		2.30	4.52	
Machilus zuihoensis var. *mushaensis*		2.18		
Sloanea formosana		2.15		
Carpinus kawakamii		2.10		
Pasania kawakamii		1.62		
Acer albopurpurascens		1.51		
Machilus zuihoensis			5.43	
Elaeocarpus japonicus			3.51	
Michelia compressa			3.20	
Cyclobalanopsis stenophylloides			2.03	4.71
Elaeocarpus sylvestris			1.81	
Cyclobalanopsis morii			1.53	19.84
Lithocarpus amygdalifolius			1.47	2.33
Trochodendron aralioides				6.90
Cyclobalanopsis sessilifolia				2.98
Neolitsea acuminatissima				1.62

FM Ficus–*Machilus* zone, *MCa Machilus*–*Castanopsis* zone, *LCy* lower *Cyclobalanopsis* zone, *UCy* upper *Cyclobalanopsis* zone

and *Castanopsis* (Fagaceae), the monsoon EBLF by species of *Castanopsis*, *Lithocarpus* (Fagaceae), *Schima* (Theaceae), and *Machilus* (Lauraceae), and the mid-montane moist EBLF by species of *Lithocarpus*, *Castanopsis*, *Cyclobalanopsis* (Fagaceae), *Manglietia*, and *Michelia* (Magnoliaceae).

The ordination of the 223 plots of Taiwan for second and third axes of DCA is shown in Fig. 2b. Axis 1 refers to the complexity of many environmental factors, and the forests were not grouped along this axis. Four altitudinal forest zones were classified along Axis 2 (eigenvalue = 0.567) from the left-hand side to the right with decreased altitude: *Ficus*–*Machilus* zone (18 plots below 500 m a.s.l.), *Machilus*–*Castanopsis* zone (45 plots at 500–1500 m a.s.l.), lower *Cyclobalanopsis* zone (85 plots at 1500–2000 m m a.s.l.), upper *Cyclobalanopsis* zone (75 plots at 2000–2500 m a.s.l.). Axis 3 may indicate a gradient of topography or soil properties. Table 2 shows the major tree species (RBA ≥1.5 %) in each forest zone. The dominant tree species in the *Ficus*–*Machilus* zone at low altitudes were *Machilus* (Lauraceae), *Ficus* (Moraceae), and *Bischofia* (Euphorbiaceae). In the *Machilus*–*Castanopsis* zone at middle altitudes, the dominant tree species were those of genera *Castanopsis* and *Cyclobalanopsis* (Fagaceae) and of *Machilus* and *Beilschmiedia* (Lauraceae). In the lower *Cyclobalanopsis* zone at middle-high altitudes, trees of *Castanopsis* and *Cyclobalanopsis* (Fagaceae), *Schima* (Theaceae), and *Machilus* (Lauraceae) were dominant, and in the upper *Cyclobalanopsis* zone at high altitudes, species of *Castanopsis*, *Cyclobalanopsis* (Fagaceae), *Trochodendron* (Trochodendraceae), and *Schima* (Theaceae) were dominant. These data clearly reveal that in Taiwan *Castanopsis cuspidata* var. *carlesii* was distributed widely along the altitude zones, while the low altitude zone (below 500 m a.s.l.) was distinguished by several species of *Ficus*, the middle altitude zone (500–1500 m) by several species of *Machilus*, the middle-high altitude zone (1500–2000 m) by *Cyclobalanopsis longinux*, and the high altitude zone (2000–2500 m) by *Cyclobalanopsis morii*.

Taxon richness

In total, 89 families, 242 genera, and 610 woody species in both the overstory and understory of the forests occurred in the 105 plots in Yunnan, including 46 families, 91 genera, and 154 species in the semi-humid EBLF (38 plots), 69 families, 169 genera, and 331 species in the monsoon EBLF (38 plots), and 49 families, 89 genera, 228 species in the mid-montane moist EBLF (29 plots; Fig. 3a–c). The monsoon EBLF had higher taxon richness values at the level of family, genus, and species than did the other two forest types. In comparison, there were a total of 82 families, 221 genera, and 533 woody species in both the overstory and understory of the forests in the 223 plots of EBLFs in Taiwan (Fig. 3d–f). We counted 68 families, 116 genera, and 186 species in the *Ficus–Machilus* zone (18 plots), 68 families, 157 genera, 326 species in the *Machilus–Castanopsis* zone (45 plots), 65 families, 147 genera, and 340 species in the lower *Cyclobalanopsis* zone (85 plots), and 57 families, 107 genera, and 286 species in the upper *Cyclobalanopsis* zone (75 plots). The taxon richness of the forests as a whole in Yunnan at the family (89) and genus (242) levels had values similar to those in Taiwan (82 families, 221 genera), while at species level the Yunnan forests had a higher taxon richness value (610) than those of Taiwan (533).

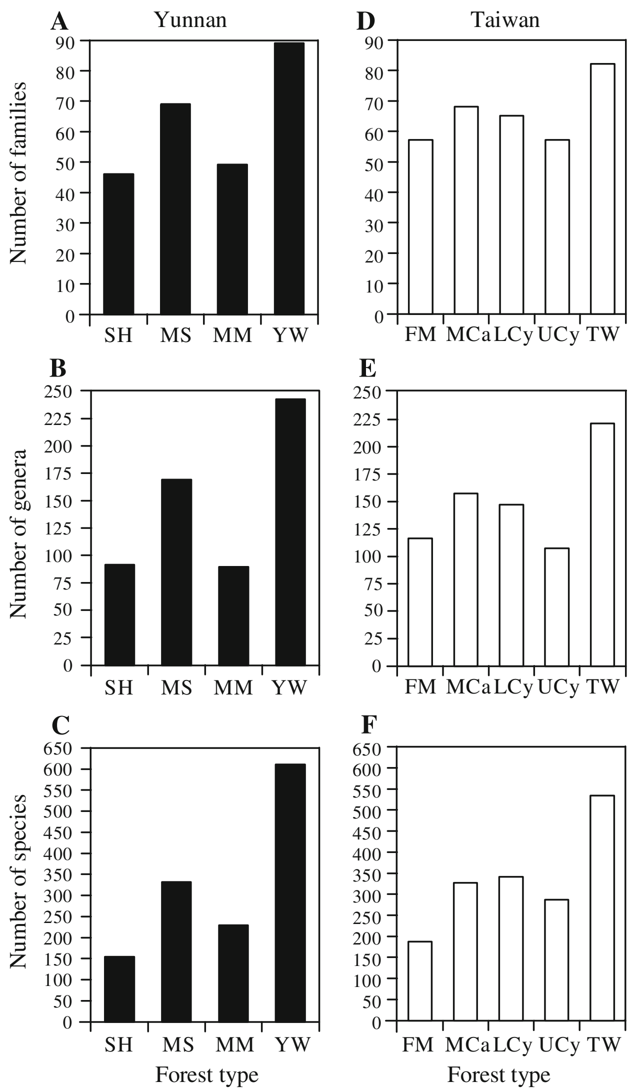

Fig. 3 Taxon richness at the family, genus, and species levels in the plots in Yunnan (**a–c**) and Taiwan (**d–f**). **a–c** *SH* Semi-humid EBLF, *MS* monsoon EBLF, *MM* mid-montane moist EBLF, *YW* EBLFs as a whole in Yunnan. **d–f** *FM Ficus–Machilus* zone, *MCa Machilus–Castanopsis* zone, *LCy* lower *Cyclobalanopsis* zone, *UCy* upper *Cyclobalanopsis* zone, *TW* EBLFs as a whole in Taiwan

The number of species within dominant families and genera was compared among the forest types/zones (Fig. 4), yielding 23, 37, and 30 Fagaceae species in the semi-humid EBLF, the monsoon EBLF, and the mid-montane moist EBLF in Yunnan, respectively, and seven, 27, 19, and 17 Fagaceae species in the *Ficus–Machilus* zone, *Machilus–Castanopsis* zone, lower *Cyclobalanopsis* zone, and upper *Cyclobalanopsis* zone in Taiwan, respectively. Fagaceae were particularly rich in the plots of Yunnan (54 species) compared to those of Taiwan (32 species). In Fagaceae, *Castanopsis* (17) and *Lithocarpus* (21) species were more abundant in Yunnan than in Taiwan (8 for *Castanopsis*, 2 for *Lithocarpus*, and 10 for *Pasania*). Similar numbers of *Cyclobalanopsis* species were found in Yunnan (11) and Taiwan (10), but there were more Lauraceae species in Yunnan (67) than in Taiwan (42). The representative genera of Lauraceae were *Machilus* and *Cinnamomum* for both regions. The EBLFs in Yunnan had a great number of Theaceae species (47) compared to Taiwan (27 species), with seven species of *Schima* in Yunnan compared to two in Taiwan. There were 11 and 20 *Moraceae* species in Yunnan and Taiwan, respectively, with only nine species of *Ficus* in Yunnan compared to 16 in Taiwan. The monsoon EBLF had a higher number (6) of *Ficus* species than did the other two forest types in Yunnan. Thirteen species of *Fiscus* were found in the *Ficus–Machilus* zone at low altitudes in Taiwan.

In total, the plots in Yunnan and Taiwan had 30 species, 96 genera, and 59 families in common. The Sørensen's similarity index (beta diversity) at the family level between the EBLFs of Yunnan and Taiwan was 0.69, at the genus level 0.41, and at the species level 0.05.

Species diversity along the environmental gradient

We applied the species richness and Simpson's diversity index to woody species (DBH ≥1 cm) in each plot to compare the forests with each other (Fig. 5). The forest types of Yunnan on the *x*-axis of Fig. 5a, b, indicate a

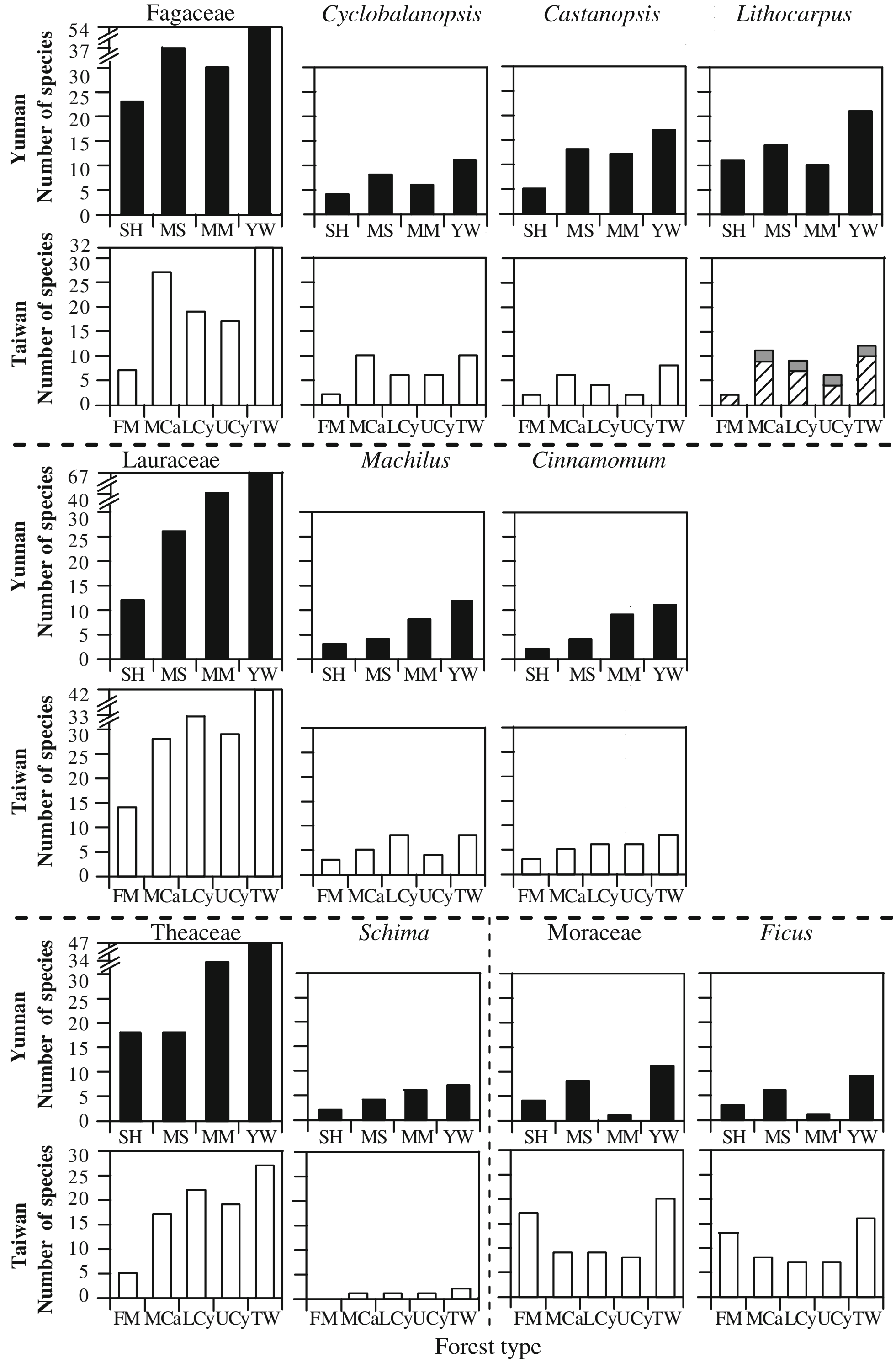

Fig. 4 Number of species of representative taxa among the EBLFs in Yunnan and Taiwan. *Gray-shaded bars Lithocarpus* in Taiwan, *bars patterned with oblique lines* are *Pasania* in Taiwan. For abbreviations, see Fig. 3

moisture gradient ranging from semi-humid to mesic-humid to moist sites. The semi-humid EBLF in Yunnan had significantly lower values of species richness (11) and Simpson's D (0.71) than the monsoon and mid-montane moist EBLFs. The monsoon EBLF in mesic–humid sites tended to have higher values (28 for species richness, 0.86 for Simpson's D) than the mid-montane moist EBLF, although the differences were not significant. In Taiwan, the forest zones in the x-axis of Fig. 5c, d, indicate an altitudinal gradient from lower (below 500 m a.s.l.) to middle (500–1500 m a.s.l.), then to mid-high (1500–2000 m a.s.l.), and finally to higher altitudes (2000–2500 m a.s.l.). The *Machilus–Castanopsis* zone in the middle altitudes (500–1500 m a.s.l.) showed significantly higher values in species richness (28) and Simpson's D (0.9) than the other forest zones.

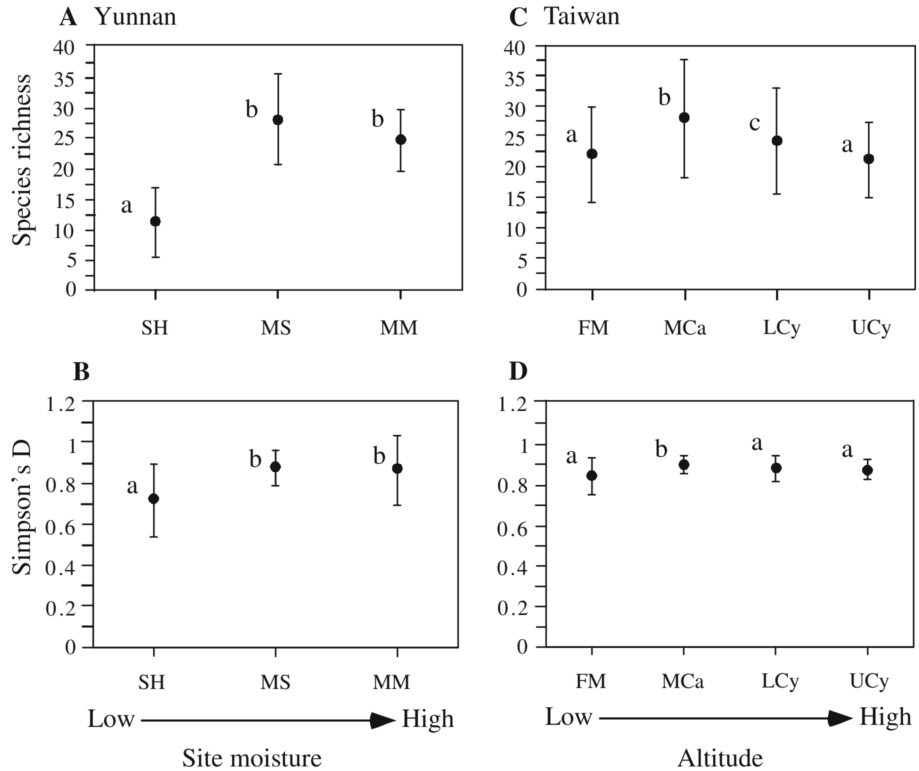

Fig. 5 Species diversity for woody species (diameter at breast height ≥1 cm). Significantly different values are indicated by *different letters*. Forests sharing the *same letters* do not differ significantly by the non-parametric Kruskal–Wallis all-pairwise comparisons test ($P < 0.0.5$). *Bar* Standard deviation. For abbreviations, see Fig. 3

Table 3 Woody species (DBH ≥1 cm) diversity (mean ± standard deviation) changes in different successional stages in Yunnan and Taiwan

Region	Forest types/zones	Area	Diversity	Forests during succession		
				Early stage	Middle stage	Late stage
Yunnan	Semi-humid EBLF	Luquan, Qiongzhusi, Xishan	*R*	7.07 ± 2.84[a] (13)	13.27 ± 2.05[b] (12)	11.40 ± 1.90[b] (12)
			D	0.57 ± 0.06[a] (13)	0.75 ± 0.03[a] (12)	0.67 ± 0.04[b] (12)
	Monsoon EBLF	Xiaoqiaogou in Wenshan	*R*	11.60 ± 1.14[a] (5)	29.10 ± 5.99[b] (7)	27.80 ± 3.70[b] (6)
			D	0.80 ± 0.03[a] (5)	0.93 ± 0.10[b] (7)	0.88 ± 0.06[ab] (6)
	Mid-montane moist EBLF	Eastern slope of Mts. Ailao	*R*	10.21 ± 3.81[a] (5)	22.09 ± 6.58[b] (7)	24.61 ± 4.46[b] (5)
			D	0.69 ± 0.01[a] (5)	0.85 ± 0.03[b] (7)	0.89 ± 0.01[b] (5)
Taiwan	*Ficus–Machilus* zone	North Central Ridge	*R*	16.72 ± 6.60[a] (6)	26.88 ± 12.21[b] (14)	21.25 ± 7.44[b] (5)
			D	0.60 ± 0.10[a] (6)	0.87 ± 0.04[b] (14)	0.83 ± 0.02[b] (5)
	Machilus–Castanopsis zone	South Central Ridge	*R*	15.11 ± 4.91[a] (9)	25.10 ± 5.43[b] (10)	23.00 ± 7.18[b] (5)
			D	0.79 ± 0.03[a] (9)	0.93 ± 0.01[b] (10)	0.89 ± 0.01[b] (5)
	Lower *Cyclobalanopsis* zone	Techi Reservoir	*R*	10.00 ± 5.90[a] (7)	23.64 ± 5.39[b] (8)	23.16 ± 7.37[b] (4)
			D	0.71 ± 0.08[a] (7)	0.90 ± 0.01[b] (8)	0.84 ± 0.03[ab] (4)

The number of plots (20 × 20 m for each) are in parenthesis. Values followed by different lowercase letters are significantly different. Forests sharing the same letters do not differ significantly by the non-parametric Kruskal–Wallis all-pairwise comparisons test ($P < 0.05$) *RBA* Relative basal area, *R* species richness, *D* Simpson's *D*

These results show that in the natural mature EBLFs, site moisture plays a large role in species distribution, composition, and species diversity in Yunnan, while the altitudinal gradient is the main controlling factor in Taiwan.

Species diversity along the successional gradient

In both Yunnan and Taiwan, secondary forests growing as coppice woods or on abandoned farmland are common in the subtropical areas. The forest succession stages can be observed in various mosaic vegetation patterns in a single area. We classified the early, middle, and late successional stages based on the structure, species composition, and the management history of the forests. In Yunnan, *Pinus yunnanensis*, *Keteleeria evelyniana*, *Alnus nepalensis*, *Populus bonatti*, *Sapium chihsinianum*, *Carpinus mobeigiana* and *Platycarya strobilaceae* were typical light-demanding pioneer species. At the early successional stage, one or several of the pioneer species dominated the plant communities.

As succession progressed, some intermediate light-demanding plants, such as *Lyonia ovalifolia*, *Rhododendron delavayi*, and *Lindera elongata*, and some shade-tolerant species, mainly those of Fagaceae, Lauraceae, and Magnoliaceae, mixed with the pioneer species. Gradually, as the forest canopy developed more closure, the short-lived light-demanding pioneer species were replaced by late successional shade-tolerant evergreen broad-leaved species such as members of *Castanopsis*, *Cyclobalanopsis*, *Lithocarpus*, *Machilus*, *Manglietia*, and *Michelia*, although some long-lived pioneer species, such as *Schima argentea* and *Schima wallichii*, were often found in mature EBLFs.

In Taiwan, *Alnus formosana*, *Acacia confusa*, *Mallotus japonicus*, *Diospyros morrisiana*, *Engelhardtia roxburghiana*, *Wendlandia formosana*, and *Zelkova serrata* were usually found in the secondary forests as the light-demanding pioneer species. During the natural recovery process of the forests, the pioneer species were gradually replaced by shade-tolerant species of *Ficus*, *Castanopsis*, *Cyclobalanopsis*, *Lithocarpus*, *Pasania*, *Machilus*, and *Trochodendron*, while long-lived pioneer species *Schima superba* was found in some mature EBLFs. The mature EBLFs contained more native and endemic plant species than did the secondary forests of Yunnan and Taiwan. An especially large number of invasive alien plants, such as *Eupatorium adenophorum*, were found in the secondary forest understory of Yunnan. Detailed data on invaders in the forest understory of Taiwan are not available.

Woody species diversity at successive stages is shown in Table 3. As shown by the species richness value and the Simpson's *D*, species diversity was significantly higher at the middle stage than earlier in both Yunnan and Taiwan. As the forest further developed, species diversity in the late stage tended to decrease except in the mid-montane EBLF in Yunnan; however, differences between the middle and late stages were not significant. As succession proceeds, the species diversity comes to resemble that of the natural mature forests.

The secondary forests, as spatially and temporally dynamic patches of vegetation showing different degrees of disturbance along the successional gradient, indicate the progress of species diversity toward the original natural patterns.

Our results demonstrate the effects of moisture, altitude, and disturbance/succession on the plant species diversity patterns in both Yunnan and Taiwan. The characteristics seen in the two forest ecosystems are summarized in Table 4.

Discussion

Phytogeographical considerations

In terms of species composition, the EBLFs of Yunnan and Taiwan consist of species distributed throughout eastern Asia from the Himalayas through southwestern, southern and eastern China to Taiwan and extending to

Table 4 Characteristics of the subtropical EBLFs of Yunnan and Taiwan

Region	Forest types/zones	Altitude (m a.s.l.)	Annual mean temperature (°C)	Annual mean precipitation (mm)	Dominants	Species diversity	Drivers of the species diversity patterns
Yunnan	Semi-humid EBLF	1500–2500	8–14	900–1200	*Cyclobalanopsis*, *Castanopsis*	Medium	Moisture, disturbance/succession
	Monsoon EBLF	800–2000	13–20	1100–2500	*Castanopsis*, *Lithocarpus*, *Schima*, *Machilus*	Very high	Moisture, disturbance/succession
	Mid-montane EBLF	2200–2900	8–15	1700–3700	*Lithocarpus*, *Castanopsis*, *Cyclobalanopsis*, *Manglietia*, *Michelia*	High	Moisture, disturbance/succession
Taiwan	*Ficus*–*Machilus* zone	< 500	15–28	1800–2500	*Ficus*, *Machilus*, *Bischofia*	High	Altitude, disturbance/succession
	Machilus–*Castanopsis* zone	500–1500	17–23	2350–3000	*Machilus*, *Castanopsis*, *Beilschmiedia*, *Cyclobalanopsis*	Very high	Altitude, disturbance/succession
	Lower *Cyclobalanopsis* zone	1500–2000	14–17	2400–2800	*Cyclobalanopsis*, *Castanopsis*, *Schima*, *Machilus*	High	Altitude, disturbance/succession
	Upper *Cyclobalanopsis* zone	2000–2500	11–14	2400–2900	*Cyclobalanopsis*, *Castanopsis*, *Trochodendron*, *Schima*	High	Altitude, disturbance/succession

southwestern Japan and of species extending from tropical Asia to eastern Asia, as well as pantropical and paleotropical species (Wu and Wu 1996; Hsieh 2002; Tang and Ohsawa 2009). Variations in species composition of forests are generally caused by two major factors: (1) climate and flora differences between areas and (2) habitat variety within an area. As a whole, the plots of the natural mature EBLFs in Yunnan and Taiwan had 59 families in common among the 89 families in Yunnan and 82 families in Taiwan, 96 genera in common among the 242 genera in Yunnan and 221 genera in Taiwan, and 30 species in common among the 610 species in Yunnan and 533 species in Taiwan. These mature EBLFs share the most dominant genera, namely, *Castanopsis* and *Cyclobalanopsis* in Fagaceae and *Machilus* in Lauraceae. The species richness of Fagaceae (54 in Yunnan, 32 in Taiwan) and Lauraceae (67 in Yunnan, 42 in Taiwan) is appreciably high in both regions. The floras of the two regions are of east Asiatic origin, formed under a typical monsoon climate. Taiwan formed part of mainland China during the Pleistocene epoch, and the vast majority of species now characteristic of the lowland Taiwanese flora must have arrived from the beginning of the Holocene onward (Shen 1994). The forests of Taiwan as a whole are less diverse in species richness, probably because of their insular character and the extensive history of land-use, although the climatic conditions in Taiwan are more favorable to evergreen broad-leaved species.

The dramatic climatic cooling and major geological events since the Tertiary should have influenced species' distribution patterns and evolution in Yunnan and Taiwan. Yunnan and Taiwan's current geographical distribution of living plants is the result of both present and past ecological and/or historical factors. An understanding of the mechanisms of the low ratio of common species between Yunnan and Taiwan will require molecular phylogeny studies.

Species diversity along the environmental and successional gradients

Variations in species diversity can be linked to several ecological gradients (Grime 1979; Huston 1994). Species diversity is related to spatial environmental heterogeneity, such as variability in habitat conditions, altitudes, and topographies (Rosenzweig 1995; Statzner and Moss 2004; Dufour et al. 2006). Our data provide evidence that site moisture is the best predictor of species composition and diversity in the EBLFs of Yunnan, while altitude plays an important role in Taiwan. The species diversity models for the two EBLF ecosystems in Yunnan and Taiwan are proposed in Fig. 6a, b. In Yunnan, the monsoon EBLF in the mesic-humid sites tends to have higher species richness and diversity. Along the altitudinal gradients in Taiwan, higher diversity is found in the forests at the middle, and middle-high altitudes. Species diversity, as influenced by temperature and precipitation, varies with altitude. As such, altitude in the EBLFs of Taiwan may be a proxy for temperature.

For forest ecosystems, various temporal trends in diversity have been observed during succession, including increases, decreases, and one or more peaks with time (e.g., Monk 1967; Habeck 1968; Auclair and Goff 1971; Peet 1978; Halpern and Spies 1995; Turner et al. 1997). Relationships between diversity and succession are complex and should be seen as system-specific. Secondary forests, under varying degrees of human disturbance, such as coppice woods or those growing on abandoned farmland, exhibit a range of stages of plant succession in both the Yunnan and Taiwan sites. The peak in diversity in the stands at the middle successional stage of each study site in Yunnan and Taiwan (Fig. 6a, b) reflects the persistence of species with varying attributes, including fast growth, slow growth, light demands, limited shade-tolerance, and greater shade-tolerance, contributing to significantly higher species diversity as compared with the early successional stage. In general, as the forest develops, species diversity in the late stage tends to decrease with the disappearance of short-lived light-demanding pioneer species (e.g., *Pinus*, *Alnus*, *Populus*, *Carpinus*, *Acacia*, *Mallotus*, and *Diospyros*); however, in our study the differences in species diversity between the middle and late successional stages were not significant, which reflects the recruitment of shade-tolerant evergreen trees (e.g., *Cyclobalanopsis*, *Castanopsis*, *Machilus*, *Ficus*, *Manglietia*, and *Michelia*)

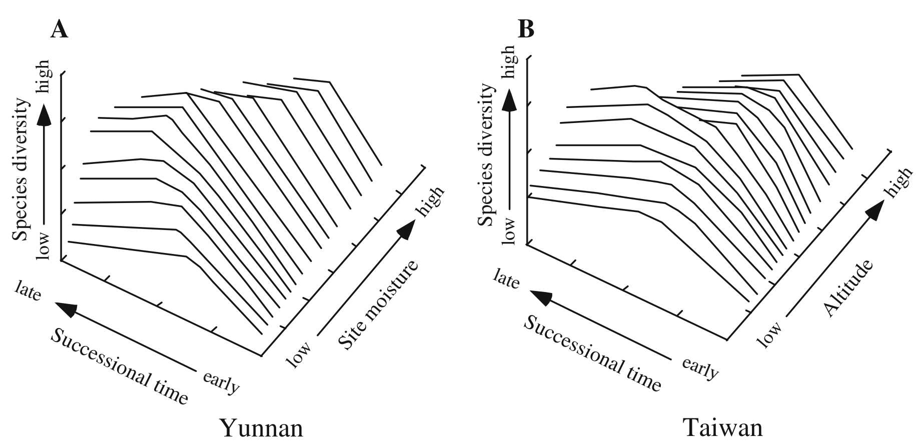

Fig. 6 Changes in species diversity with site moisture and successional time in the EBLFs of Yunnan (**a**) and Taiwan (**b**)

into the overstory. As our understanding of the growth and development of forests increases, it becomes clear that natural succession processes, as opposed to human interference, such as plantations, is the most efficient way towards achieving reestablishment and the accompanying ecological benefits.

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