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FOREST DIVERSITY AND COMMUNITY DYNAMICS ALONG AN ALTITUDINAL GRADIENT OF AILAOSHAN MOUNTAIN (YUANYANG, YUNNAN PROVINCE, CHINA)

Yuan Li[a], Yanqun Zu[a], Bozhi Wu[b], Guoqing Gao[a], Fenggen Guo[b]
[a]*College of Resources and Environment, Yunnan Agricultural University, Kunming, China*
[b]*College of Agronomy and Biotechnology, Yunnan Agricultural University, Kunming, China*

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Abstract. In order to evaluate forest community diversity, the quantity of forest community succession along an altitudinal gradient from 1690 to 2016 m above sea level, the understanding of relationships between diversity and community dynamics, and data from sampling plots of forest communities were studied. Forest communities were mid-mountain moist evergreen broad-leaved forests on the southern slope of the Ailaoshan Mountain in Yuanyang County (near the Hani terraces) in Yunnan Province, China. The results showed that (1) the mean species richness, ecological dominance, and evenness (*E*) were 9.16, 0.31, and 0.27, respectively. The mean Shannon-Wiener Index and Coverage Weighted Foliage-Height Diversity Index were 0.84 and 0.41, respectively. (2) The mean live aboveground biomass (AGS) was 99.23 Mg/ha and the mean Composition Index (CI) was 182.17. Species diversity (including *E*, richness, and Shannon-Wiener Index), live AGS, and CI could be predicted by the mid-domain effect (MDE), which displayed a unimodal pattern against elevation. (3) Richness, *E*, Shannon-Wiener Index, and Coverage Weighted Foliage-Height Diversity Index increased with CI. Ecological dominance decreased with increased CI, following a quadratic relationship. Whittaker Index decreased with both increased CI and AGS, with a quadratic relationship. Much forest diversity could be explained by the MDE. However, forest dynamics were seriously disturbed by human activities. More attention should focus on increasing forest diversity in order to prevent the degradation of forest ecological functions thus resulting in threats to the sustainable development of the local ecological systems.

Keywords: landscape management, forest diversity, community dynamics, altitudinal gradient, Ailaoshan Mountain.

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Introduction

Biodiversity is an important attribute of ecosystem function. Forest community diversity usually increases with time and succession to a peak and then declines toward a stable climax community (Odum 1969; Niemela 1997). Many studies on succession patterns have focused on plants and organisms (Whittle *et al.* 1997; Wang *et al.* 2006). Forest communities are in specific successional stages. Thus, it is necessary to discover the relationship between community dynamics and diversity, quantifying the succession of forest community. Composition Index (CI) and biomass are used to quantify forest community succession (Curits, McIntosh 1951; Alves *et al.* 2010).

Biodiversity includes genetic, species, ecosystem, and landscape diversity (Franklin 1988; Li *et al.* 2001). The indices α-diversity and β-diversity are useful for evaluating forest community diversity (Whittaker 1960, 1975). The Index α-diversity expresses biodiversity inside the community, including the Species Richness Index, Species Evenness Index, Shannon-Wiener Index, Simpson Index, horizontal structure diversity, and vertical structure diversity (Magurran 1988). The Index β-diversity expresses diversity among communities, including the Whittaker Index (Whittaker 1960), Cody Index (Cody 1975), Wilson-Shmida Index (Wilson, Shmida 1984), and Jaccard Index (Tang *et al.* 2007). The spatial distribution of biodiversity has long been a key issue in ecology and biogeography (Lomolino 2001; Whittaker *et al.* 2001; Niu *et al.* 2008). Many reports focused on diversity, species, and area along latitudinal gradients (Stevens 1989; Kerr 1999). More attention is now paid to diversity along altitudinal gradients, because of the misunderstandings based on perceptions

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Corresponding author. Yanqun Zu
E-mail: zuyanqun@yahoo.com.cn

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that biodiversity decreased with both latitude and altitude (Rahbek 1997, 2005; Zhao *et al.* 2009).

The mid-domain effect (MDE) is an important mechanism influencing species diversity along altitudinal gradients (Colwell, Lees 2000; Sanders 2002; Bachman *et al.* 2004; Colwell *et al.* 2004; Kattan, Franco 2004). Colwell and Lees 2000 reported on the MDE, in which plant species diversity reached the maximum in middle elevation regions (Lieberman *et al.* 1996; Tang, Ohsawa 1997; Feng *et al.* 2006). Research suggests that diversity is related to the size of the research area, the total altitudinal range of mountains, plant species composition, and species characteristics (Hu *et al.* 2007; Niu *et al.* 2008).

The aims of this study were to (1) evaluate forest community diversity along an altitudinal gradient; (2) evaluate the quantity of forest community succession along an altitudinal gradient; and (3) understand the relationships between diversity and community dynamics.

1. Materials and methods

1.1. Study site and sampling design

The study sites were located on the southern slope of the Ailaoshan Mountain, which is in the transition zone between the Yunnan Plateau and Western Hengduanshan Mountain (an extension of the Qinghai-Tibet Plateau), and the transition between the middle and southern subtropics. The forest is a mid-mountain moist evergreen broad-leaved forest, in which *Fagaceae, Lauraceae, Magnoliaceae* and *Theaceae* are the dominant species with an average height of 9–9.8 m and stem area at breast height 125–138 cm^2 (He *et al.* 2000; Niu *et al.* 2008). The forest community has a complex floristic composition, and three conspicuous layers: arbor layer, shrub layer, and herbage layer. The richness of interlayer plants is very high (Yang *et al.* 2010a).

This study was conducted on a mountainous, steeply sloping circa 1200 ha site near the Hani terraces, Xinjie town in Yuanyang County, Yunnan Province, China (102°43′38.7″–102°46′24.1″E, 23°05′45″–23°07′32.7″N) at 1547–2019 m above sea level. Local soils are the subtropical red soils (Yuan *et al.* 2010). The climate is a subtropical monsoon, with rainy (May–October) and dry (October–May) seasons. Most of the annual precipitation (circa 1398 mm) falls during the rainy season. The mean temperature is 16.4 °C, ranging from 32.4 to −2.6 °C.

This study was carried out during March–November 2009. Forty typical plots (20 × 20 m) were selected, representing 10 major community types along the altitudinal gradient (Fig. 1 and Table 1). Ten tropical communities were dominated by *Choerospondias axillaris* (Roxb.) Burtt. et Hill., *Helicia clivicola* W.W. Smith., *Lindera communis* Hemsl., *Clerodendrum bungei* Steud., *Neolitsea chuii* Merr., *Cunninghamia C. lanceolata* (Lamb.) Hook., *Castanopsis carlesii* (Hemsl.) Hayata, *Pinus yunnanensis* Franch., *Mallotus barbatus* (Wall. ex Baill.) Muell.-Arg., and *Alnus nepalensis* D. Don. (Table 1). Four replicate plots of each community type were at the same altitude. In each plot, the following data were collected: altitude, plant species, plant density, total coverage, tree coverage, shrub coverage, grass coverage, total height, shrub height, grass height, wood diameter at breast height, number of species, and number of individuals for every identified species.

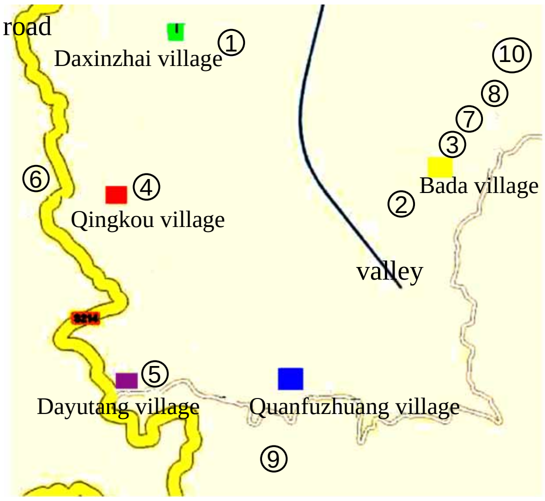

Fig. 1. The map of sampling sites

1.2. Measurement of diversity

1.2.1. α-diversity

Species diversity. Species diversity was calculated using the following indices: Shannon-Wiener Index (H'), importance value (IV_i), species richness (SR), ecological dominance (ED), and evenness (E) (Li *et al.* 2001). The equations for these indicators are:

$$H' = -\Sigma p_i \ln p_i, \quad (1)$$

Table 1. The dominant species and elevation of communities

Sampling No.	Dominant species in community type	Elevation (m)
1	*Choerospondias axillaris*	1690
2	*Helicia Clivicola*	1750
3	*Lindera communis*	1781
4	*Clerodendrum bungei*	1813
5	*Neolitsea chuii*	1876
6	*Cunninghamia lanceolata*	1899
7	*Castanopsis carlesii*	1938
8	*Pinus yunnanensis*	1960
9	*Mallotus barbatus*	1982
10	*Alnus nepalensis*	2016

where H' is the value of the Shannon-Wiener Index and p_i the proportion of the ith species, $p_i = n_i/N$.

$$IV_i = (\mathrm{RD}_i + \mathrm{RC}_i + \mathrm{RF}_i)/3, \qquad (2)$$

where IV_i is the importance value Index of the ith species and RD_i, RC_i, and RF_i are relative density, relative coverage, and relative frequency of the ith species, respectively.

$$\mathrm{SR} = (s-1)/\lg N, \qquad (3)$$

where N is the total number of species in the community and s the total species number.

$$\mathrm{ED} = \Sigma n_i(n_i-1)/N(n_i-1), \qquad (4)$$

where N is the total number of species in the community and n_i the number of the ith species.

$$E = H'/\ln s, \qquad (5)$$

where H' is the value of the Shannon-Wiener Index and $\ln s$ the maximum H', s the total species numbers.

Vertical structure diversity. The vertical structure diversity is calculated using the Coverage Weighted Foliage-Height Diversity Index and the equation is (Wang *et al.* 2006):

$$H_c' = -\Sigma(C_i/C\cdot H_i/H)\ln(C_i/C\cdot H_i/H), \qquad (6)$$

where H_c' is the Coverage Weighted Foliage-Height Diversity Index, C_i is the coverage of the ith foliage-height, C the total coverage of community, H_i the height of the ith foliage-height, and H is the total height of the community.

1.2.2. *β-diversity*

$$\text{Whittaker Index}\,(\beta_\omega) = S/(m_a-1), \qquad (7)$$

where S is the total number of species in the community and m_a is the mean number of species of plots (Li *et al.* 2001).

$$\text{Jaccard Index}\,(C_j) = j/(a+b-j), \qquad (8)$$

where a and b are the total number of species for the two communities, j is the number of common species among the two communities. The Jaccared Index was used to compare each of the different nonclimax plant communities to the climax forest, which was middle-mountain moist evergreen broad-leaved forest in the vertical vegetation zone of a subtropical mountain in Yuanyang County, Yunnan Province, China.

1.3. Quantification of community dynamics

CI and live above-ground biomass (AGS) were used to quantify community dynamics (Curits, McIntosh 1951). CI is the product of the IV_i and the climax adaptation value (CAV_i):

$$\mathrm{CI} = \Sigma \mathrm{IV}_i \cdot \mathrm{CAV}_i. \qquad (9)$$

CAV_i values in the southern area of evergreen broad-leaved forest of Yunnan Province are listed in Table 2, as reported by Wang (1987). The values of CAV_i are 1, 3, 5, 7, and 9 for pioneer species, secondary pioneer species, transitional species, secondary climax species, and climax species, respectively.

Table 2. The climate adaptation values (CAV_i) of relatively important trees in the southern area of evergreen broad-leaved forest of Yunnan Province, China

Dominant species	important valuve (IV_i)	Climax adaptation value (CAV_i)
Choerospondias axillaris	21.25	7
Helicia Clivicola	41.19	9
Lindera communis	34.25	9
Clerodendrum bungei	15.06	9
Neolitsea chuii	15.55	9
Cunninghamia lanceolata	65.05	1
Castanopsis carlesii	38.65	9
Pinus yunnanenis	67.81	1
Mallotus barbatus	33.24	5
Alnus nepalensis	71.60	1

Estimation of live AGS

The plot census data (tree stem ≥4.8 cm) were used to estimate stand volume (M) and AGS using an allometric equation, which was a model developed by Zeng (2005) for forest types in Yunnan. The equation is:

$$M = G\cdot H\cdot F, \qquad (10)$$

where M is the stand volume, G is the stem area at breast height per hectare, H is the mean tree height, and F is the mean form-factor of the tree species (0.472).

$$\mathrm{AGS} = a\cdot M + b, \qquad (11)$$

where AGS is the live AGS, M is the stand volume, a and b are constants based on values estimated by Fang *et al.* (2001) and Zeng (2005) (Table 3).

Table 3. The a and b values for calculation of M and AGS

Tree species	*a*	*b*
Pinus yunnanenis	0.5101	1.0451
Cunninghamia lanceolata	0.3999	22.5410
Broad-leaved tree	0.4754	30.6034

1.4. Statistical analysis

Effects of altitude were examined by a linear regression, using altitude as the independent variable. Means were used when samples were replicated within a site. Differences between altitudes with multiple comparison were tested using one-way analysis of variance (ANOVA) whenever samples were replicated at each site. Least significant difference (LSD) was used for determining significant differences between properties. SPSS (11.5) and EXCEL (2003) software were used for statistical analysis.

2. Results and discussion

2.1. Community diversity distribution

The total number of forest species was 181, belonging to 73 families and 103 genera in the research area with altitudinal from 1547 to 2019 m above sea level. The typical climax community was *Neolitsea chuii* community, dominated by *Neolitsea*, *Lithocarpus*, *Castanopsis*, and *Schima*. The dominant species of shrubs were *Melastoma normale* D. Don., *Sinocalamus affinis* (Rendle.) McClure and *Camellia pitardii* Coh. stuart, and dominant species of grasses were *Arthraxon hispidus* (Thumb.) Makino, *Gnaphalium affine* D. Don., *Eupatorium coelestrium* L., *Centella asiatica* (L.) Urban, *Selaginella uncinata*, and *Commeline communis* L.

The total number species of every community (*N*), SR, ED, *E*, Shannon-Wiener Diversity Index (*H'*), Coverage Weighted Foliage-Height Diversity Index (H_c'), and β-diversity *(*β_ω and C_j*)* are shown in Figure 2. Differences in *N*, SR, ED, *E*, *H'*, H_c', β_ω, and C_j were observed in each community.

The data trends for richness and number of species were similar with altitude (Fig. 2a). Mean SR was 9.16 and SR and *N* at altitudes <1938 m were more than at altitudes >1938 m, except for the community *M. barbatus* at 1982 m. Mean ED and *E* were 0.31 and 0.27, respectively, with opposing trends. ED (0.08–0.16) was stable for 1750–1876 m, <1690 m (0.34), and <1899 m (0.54), except for the community *C. carlesii* (0.25) (Fig. 2b).

The trends of the Shannon-Wiener Index and Vertical Structure Diversity Index were similar with altitude (Fig. 2c). Mean *H'* was 0.84, ranging from 0.42 to 1.38. *H'* was stable (1.13–1.38) from 1750 to 1876 m, and <0.80 at 1690 m and >1899 m. Mean H_c' was 0.41, ranging from 0.17 to 0.68. The trends of β_ω and C_j were similar. Mean β_ω was 10.12 (mainly 5–10), except for the community *C. carlesii* (25.86) (Figs 2d and e). Mean C_j was 0.23 (mainly 0.14–0.21), except for the communities *C. carlesii* (0.04), *Pinus yunnanenis* (0.05), and *Neolitsea chuii* (1.00).

Analysis of forest diversity focused on α-diversity and β-diversity. α-Diversity is intracommunity species diversity and vertical structure diversity (including richness, *E*, ED, Shannon-Wiener Index, and Vertical Structure Diversity Index). β-Diversity expresses intercommunity diversity and includes β_ω and C_j (Li *et al.* 2001; Wang *et al.* 2001).

From 1750 to 1876 m, species diversity indicators remained relatively stable. Richness, *E*, and Shannon-Wiener Index from 1750 to 1876 m above sea level were greater than at other elevations, while ED showed the opposite trend. It is suggested that communities at 1750–1876 m would be the dominant and representative community. Ailaoshan Mountain is in the transition region of the middle and southern subtropics (Yuan *et al.* 2008). Typical representative forest in the Ailaoshan Mountain is the middle-mountain moist evergreen broadleaved forest, dominated by *Lithocarpus* and *Castanopsis* (Xie *et al.* 1996; Tang *et al.* 2007; Yang *et al.* 2010b). Dominant species were *Lithocarpus xylocarpus*, *Castanopsis rufes*, *Lithocarpus hancei*, and *Schima noronhas* (He *et al.* 2000; Li *et al.* 2006, 2007; Yuan *et al.* 2008, 2010). In the research area, the dominant species were *H. clivicola*, *L. communis*, *C. bungei*, *Neolitsea chuii*, *Schima superba*, *A. nepalensis*, *Camptotheca acuminata*, and frequently *Lindera Thunb.* The community *N. chuii* was particularly diverse, with 45 plant species, the highest richness, *E*, Shannon-Wiener Index, and the lowest ED. The community *N. chuii* was considered to be the typical zonal vegetation climax.

Species diversity indicators were less for the community *C. axillaris* at 1690 m than at 1750–1876 m. This might be due to human disturbance, as they are adjacent to the Hani villages, which are located in the mid-mountain area, at 1600–1700 m. Similar disturbances may have affected communities >1899 m. Communities dominated by *Cunninghamia C. lanceolata*, *Pinus yunnanenis*, and *A. nepalensis* were typical secondary communities, with only one dominant species. On the one hand, the invasive species *Eupatorium coelestrium* grew rapidly and restrained other plant species, resulting in restoration difficulty and low species diversity (Ding *et al.* 2007; Guo, Cheng 2008; Liao *et al.* 2008; Chen 2009). On the other hand, *Camellia sinesis* O. Ktze and *Amomum medium* Lour were planted in those communities to increase income, leading to the loss of natural plant species and simpler community structures (Lin 2003; Li *et al.* 2008; Liao *et al.* 2008).

β_ω remained relatively stable, with no significant differences of β_ω between the four communities at 1750–1876 m. The community *C. carlesii* was seriously disturbed in this area, due to fuelwood removal. The β_ω of the *C. carlesii* community was higher than that of other communities, due to the shrub and tree layers being seriously disturbed by human activities.

Community diversity is affected by many factors, including soil type, elevation, temperature, rainfall,

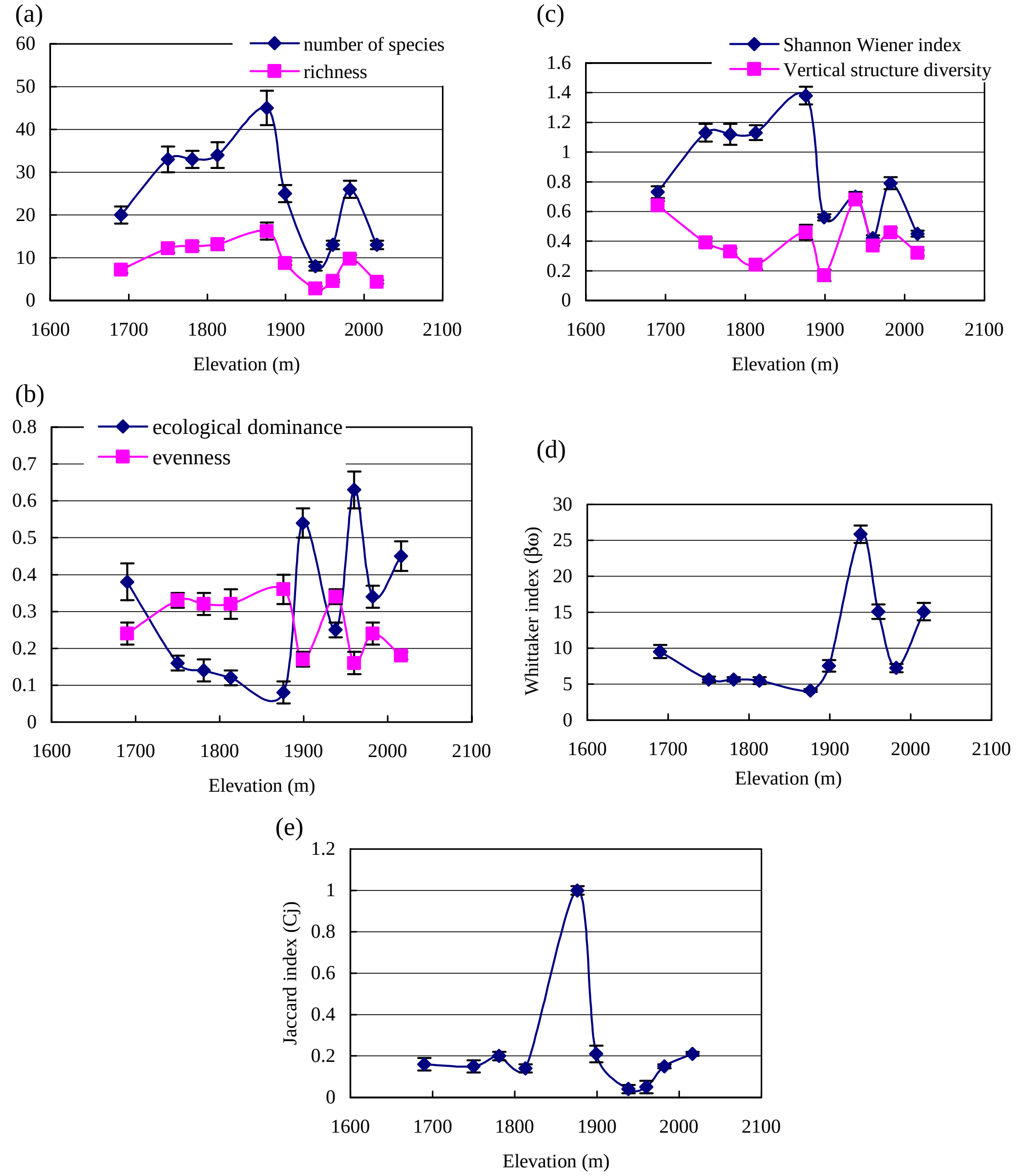

Fig. 2. Values of number species of every community (N), species richness (SR), ecological dominance (ED), evenness (E), Shannon-Wiener diversity index (H'), coverage weighted foliage-height diversity index (H_c') and β-diversity (β_ω and C_j) for each community with altitude

and human disturbance (Kucas 2010). Species diversity (including E, richness, and Shannon-Wiener Index) predicted by the MDE first increased and then decreased after reaching their maximum, showing a unimodal pattern against altitude. The MDE showed that species diversity maximized at mid-altitudes. Niu *et al.* (2008) also reported on the distribution of species diversity, in which height and diameter at breast height adopted a single peak pattern along an altitudinal gradient in the Ailaoshan Mountain area. The maximum values of Shannon-Wiener Index and SR occurred at circa 2000 m in semi-moist evergreen broad-leaved forest on the western and eastern slopes of the Ailaoshan Mountain. The distribution of species is successive and distribution area of different species overlap each other, based on the MDE (Colwell, Lees 2000; Zheng *et al.* 2009). The overlapped species are abundant, associated with suitable temperature and rainfall in the mid-altitude region, resulting in high species diversity. Species diversity decreased at both relatively low and high altitudes and was mainly due to few overlapping species, unsuitable temperatures, low soil fertility, and prolonged human disturbance (Tilman *et al.* 1996; O'brien *et al.* 2000).

2.2. Community dynamics variation

Mean AGS was 99.23 Mg/ha (range 34.98–227.15) (Fig. 3). AGS decreased with altitude, except for the

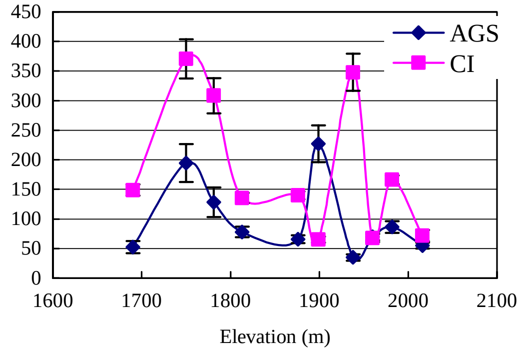

Fig. 3. Composition index (CI) and live aboveground biomass (AGS*)* for each community with altitude

community *C. axillaris* at a relatively low elevation (1690 m) and the community *Cunninghamia C. lanceolata* at 1938 m. Mean CI was 182.17 (range 65.05–370.71). The trend for CI was similar to AGS (Fig. 3). CI decreased with altitude, except for communities at relatively low altitude (1690 m) and the community *C. carlesii* at 1938 m.

The live AGS and CI also followed a unimodal pattern, increasing and then decreasing after reaching their maximum values. This trend is explained by the MDE (Whittaker, Heegaard 2003; Hu *et al.* 2007). AGS and CI reached their maximum at mid-altitude (1750 m). However, the AGS of the community *Cunninghamia C. lanceolata* was an exception, with 227.15 Mg/ha at 1899 m, which was more than that in the community at 1750 m (194.48 Mg/ha). The reason was that most *Cunninghamia C. lanceolata* were planted and managed for well over 10 years by farmers for economic income. Most *Cunninghamia C. lanceolata* were tall and robust, with a mean stem area at breast height of 73.49 m^2/ha.

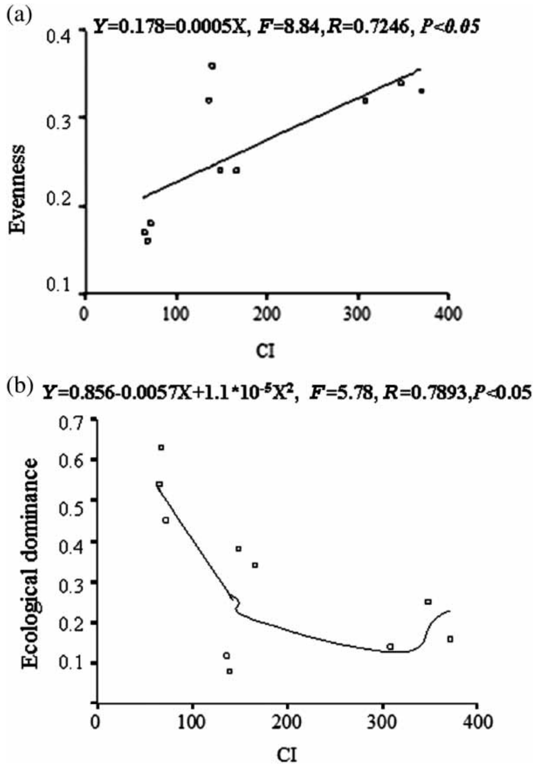

Fig. 4. The relationships between composition index (CI) and evenness (*E*), ecological dominance (ED) ($n = 10$)

The CI of the community *C. carlesii* was an exception, with CI 347.82, which was the second highest CI and just less than that in the community at 1750 m. The reason was mainly due to *C. carlesii* being the representative dominant tropical plant species in subtropical evergreen broad-leaved forest with the climax adaptation value of 9. The community *C. carlesii* was located at 1938 m on the southwest slope, in a sunny aspect. The CI of the community *C. carlesii* was high, but succession was considerably restrained by human disturbance.

2.3. Effect of community diversity and elevation on dynamics variation

A positive linear relationship was observed between *E* and CI (Fig. 4a). *E* increased with CI, which meant *E* had the similar tendency as community dynamics. Ecological dominance decreased with increased CI and increased slightly in the quadratic curve (Fig. 4b). The turning point with ED 0.14 and CI 308.25 was community *L. communis.*

Richness increased with CI, except for one specific point with the lowest richness 2.79 and CI 347.82, which was community *C. carlesii* strongly disturbed due to fuelwood removal (Fig. 5a). The Shannon-Wiener Index was low in the early community succession (Fig. 5b). The *H'* increased with CI and became stable at the stage of nearing the community climax, except for two specific points, one of which was climax community *N. chuii* with the highest *H'* 1.38 and CI 139.92. The other was *C. carlesii* community with *H'* 0.7 strongly disturbed by human activities. It is postulated that the maximum species diversity index occurs before the community climax is achieved. The H_c' increased with CI except for two specific points, which were community *H. clivicola* with H_c' 0.39 and the highest CI 370.71 and community *L. communis* with H_c' 0.33 and CI 308.25 strongly disturbed by human activities and invasion species (Fig. 5c). The vertical structure became abundant as the community approached the climax state.

β_ω (which is β-diversity associated with the intracommunity), decreased with increased CI except for one point, which was community *C. carlesii* with the highest β_ω 25.86 strongly disturbed by human activities (Fig. 6a). β_ω decreased with increased AGS and increased slightly in the quadratic curve (Fig. 6b), which followed a similar trend to ED. It is suggested that species composition among communities become more uniform as communities approach

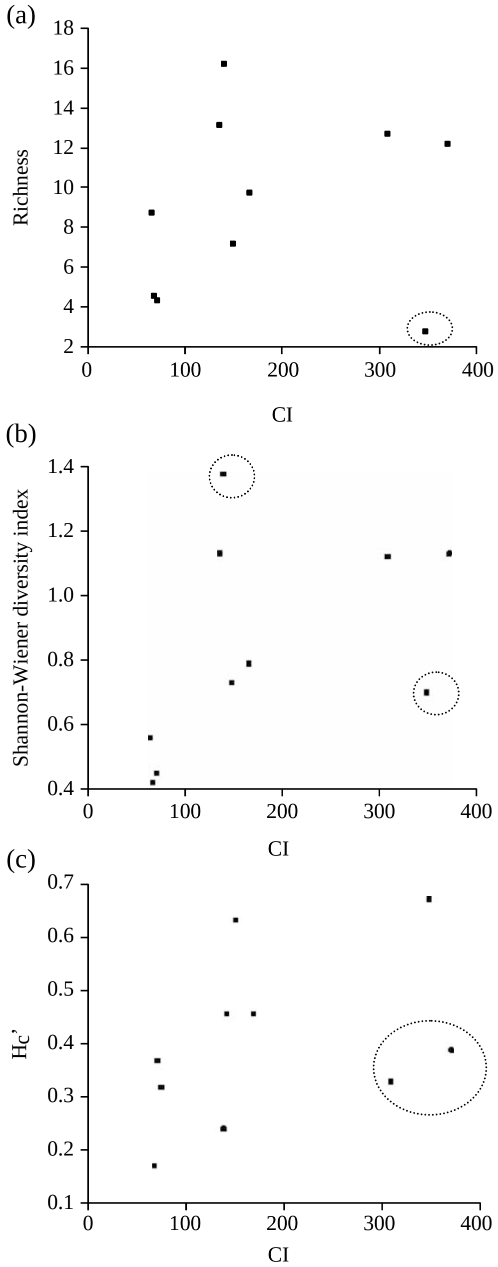

Fig. 5. Relationships among composition index (CI), species richness (SR), Shannon-Wiener diversity index (H'), and coverage weighted foliage-height diversity index (H_c')

the climax state. With the community approaching the climax, every species will be its own niche within the community.

Considering the relationships between forest diversity and dynamic variation, E, richness, Shannon-Wiener index, and vertical structure, the diversity index increased with CI and ED decreased with increased CI. This is because the dominant species become progressively less important as the community approaches the climax state and every species will be its own niche within the community, with the opposite trend to ED and E (Magurran 1988; Wang *et al.* 2006). Meanwhile, in the early stage of community succession, the niches

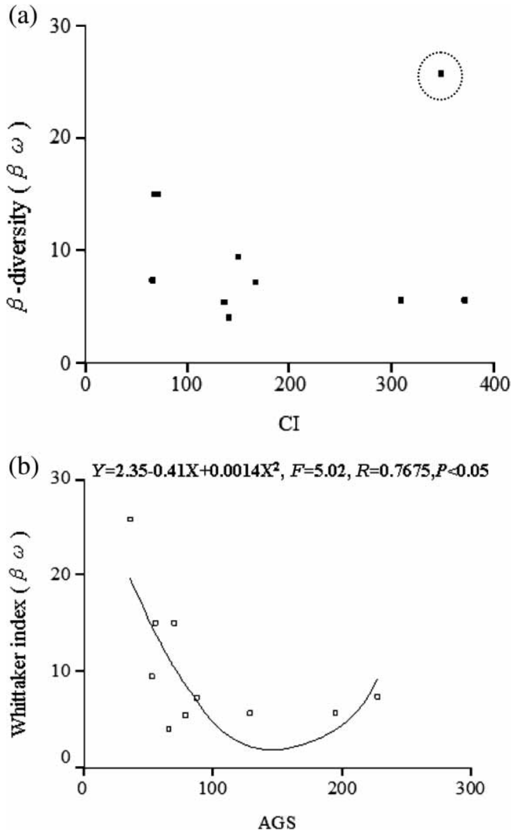

Fig. 6. Relationships between composition index (CI), live aboveground biomass (AGS), and β-diversity (β_ω) ($n = 10$)

of species overlapped, and interspecies and intraspecies competition is very strong. With community succession, every species retains its own niche and vertical diversity increases (Feng *et al.* 2006). The community *N. chuii* was a climax community and more attention should be paid to community species diversity, succession, slope direction, and human disturbance. β-diversity decreased with increased CI and AGS with the quadratic curve. With the community approaching the climax state, every species will be its own niche within the community (Whittaker 1960; Li *et al.* 2001).

Conclusions

The typical climax was *N. chuii* community in the research area with altitudinal from 1547 to 2019 m above sea level. The forest community diversity and succession along an altitudinal gradient and its relationships were as following:

1. Mean SR, ED, and E were 9.16, 0.31, and 0.27, respectively. The mean Shannon-Wiener Index was 0.84, ranging from 0.42 to 1.38. The Mean Coverage Weighted Foliage-Height Diversity Index was 0.41, ranging from 0.17 to 0.68. The mean live AGS was 99.23 Mg/ha, ranging from 34.98 to 227.15 Mg/ha. The mean CI was 182.17, ranging from 65.05 to 370.71.

2. Species diversity (including E, richness, Shannon-Wiener index, live AGS, and CI) could all be

predicted by the MDE, increasing first and then decreasing after reaching their maximum, showing a unimodal pattern with altitude.

3. The richness, *E*, Shannon-Wiener Index, and Coverage Weighted Foliage-Height Diversity Index increased with CI. Species diversity and vertical structure diversity became more abundant as the community approached the climax state.

4. Ecological dominance decreased with increased *CI* in a quadratic relationship. β_ω decreased with increased *CI* and *AGS* in a quadratic relationship. As the community approached the climax state, every species would be its own niche in the community.

Forest diversity, especially species diversity, retained natural characteristics and was influenced by the MDE. However, the forests were seriously disturbed by human activities. It is suggested that decreased forest diversity (including species diversity and vertical structure diversity) would degrade forest ecological functions and threaten the sustainable development of local ecological systems.

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Yuan LI. Dr, Professor at the College of Resources and Environment, Yunnan Agricultural University. He received his PhD in Ecology in 1998 from Lanzhou University, China. Publications: author/co-authors of ~80 scientific papers. Research interests: community ecology, pollution ecology, and ecological restoration.

Yanqun ZU. Dr, Professor at the College of Resources and Environment, Yunnan Agricultural University. She received her PhD in Agronomy and Biological Engineering in 2008 from Gembloux Agricultural University, Belgium. Publications: author/co-authors of ~60 scientific papers. Research interests: environmental ecology, ecological restoration, and water and soil conservation.

Bozhi WU. Dr, Professor at the Department of Agronomy and Biotechnology, Yunnan Agricultural University. He received his PhD in Water and Soil Conservation in 2000 from Wolverhamton University, UK. Publications: author/co-authors of ~80 scientific papers. Research interests: water and soil conservation and agricultural ecology.

Guoqing GAO. is an MA student at the College of Resources and Environment, Yunnan Agricultural University. He received his Bachelor's degree in Environmental Science in 2009 from Yunnan Agricultural University. Publications: author of one scientific paper. Research interests: water and soil conservation and forest ecology.

Fenggen GUO. Dr, Professor in the Department of Agronomy and Biotechnology, Yunnan Agricultural University. He received his PhD in Botany in 1998 from Zhejiang University, China. Publications: author/co-authors of ~60 scientific papers. Research interests: water and soil conservation and botany.