

研究報告

種豐富度模式應用於惠蓀林場小出山闊葉樹次生林之植群動態分析

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【摘要】本研究藉由幾何序列、對數序列、截斷對數常態分布模式、折枝模式等四種不同性質的種豐富度模式，剖析1983~1997年間，惠蓀林場小出山之三種疏伐處理的闊葉樹次生林之植群動態。研究結果得知各時期之不同處理間的 α 、 λ 的種豐富度指數並無差異；此外，以最符合之種豐富度模式而言，不同時期之三種處理多最符合對數序列，其次為幾何序列、截斷對數常態分布模式，僅少數樣區最符合折枝模式。整體而言，1983年(處理前)乃至1997年(處理後13年)，此三種處理之各樣區的植群結構僅具細微變動，多數樣區處於演替中後期階段，而部分樣區已達極盛相。

【關鍵詞】種豐富度模式、幾何序列、對數序列、截斷對數常態分布模式、折枝模式。

Research paper

Analyzing Vegetation Dynamics of the Broad-leaved Secondary Forest by Species Abundance Models at Mt. Showchu in the Hue-Sun Forest Station

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【Summary】It was little known about the vegetation dynamics of the broad-leaved secondary forest at Mt. Showchu in central Taiwan. In this study, species abundance models such as geometric series, logarithmic series, truncated log normal distribution, and broken stick model were applied to analyze the change in biodiversity of 1983 to 1997. It showed no significant difference on the species richness indices for α and λ of broad-leaved secondary forests among the various periods. Furthermore, the logarithmic series was the best fit model for the outcomes of three different thinning treatments applied to the target experimental area in four investigation periods, followed by the geometric series and then the truncated log

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normal distribution. The broken stick model hardly fit the actual dynamics. Therefore, it was found that after 13 years of the experiment, the three thinning treatments had some minute effect on the dynamics of the vegetation structures in the plots. Most plots were in the middle and later stages of the succession, whereas other plots approached the climax.

【Key words】 species abundance model, geometric series, logarithmic series, truncated log normal distribution, broken stick model.

INTRODUCTION

The Third Forest Resources and Land Use Inventory in Taiwan showed that the coverage of forests on the island of Taiwan was about 59%, and 1,121,400 ha were broad-leaved forests which accounted for 31.19% of total land area (Goan and Chen, 1995). Some of these forests became secondary forests due to natural or human disturbances. Therefore, it is essential to realize the development of these broad-leaved secondary forests.

In a broad sense, secondary forests form successively from original forests through natural forces such as big storms or severe changes in climate, or through human disturbances. Chen *et al.* (1994) indicated when the original forests were destroyed repeatedly on a large scale (e.g., reckless cutting, burning, reclaiming, converting to pastures, etc.), naturally secondary communities formed through secondary succession on the secondarily exposed land. So the secondary forest had a very different environment from the original forest. And the original communities would be replaced by the secondary communities. On the other hand, Wu *et al.* (1991) postulated that secondary forest ecosystems formed successively from original forest ecosystems due to human disturbances. But, traces of original forests could still be found either in the biological species and compositions or the non-biological environmental factors.

The environmental factors such as micro-climate and soil physical-chemical quality in secondary forests differed from those in original forests. The plants, animals, and the surrounding environment in a secondary forest constituted an undivided and complex synthesized unit. This was called a secondary forest ecosystem. For forest ecologists, besides investigating the conversion between materials and energy among the constituents, it was even more important to understand the characteristics of these secondary forest ecosystems. It included time series and space structures, ecological status and conversion efficiency between materials and energy of the organisms, and balance mechanisms and stability limit. Therefore, four widely used species abundance models were applied in this research to study the dynamic changes in the structures of the vegetation in the experiment plots. It was expected to obtain valuable information on vegetation succession that could be applied on management, planning, and policy-making to broad-leaved forests in the future.

MATERIALS AND METHODS

Description of study area

The study area was the broad-leaved secondary forests on No. 224 plantation of the compartment 3 and 4 in the Hue-Sun Forest Station owned by National Chung Hsing University (NCHU). The total area was 27.36

ha (Tsai *et al.* 2000). It was originally a broad-leaved forest composed of typical Lauro-Fagaceae association in Taiwan. The dominant species in the forest were *Cinnamomum subavenium*, *Machilus thunbergii*, *Litsea acuminata*, *Cyclobalanopsis longinux*, *Castanopsis eyrei*, *Castanopsis kawakamii*, *Pasania nantoensis*, *Engelhardtia roxburghiana*, etc. The subdominant species were *Rhododendron formosanum*, *Syzygium formosanum*, *Glochidion acuminatum*, *Mallotus paniculatus*, *Alniphyllum pterospermum*, *Neolitsea acuminatissima*, *Dendropanax pellucidopunctata*, *Meliosma rhoifolia*, *Syzygium buxifolium*, etc. Lin (1956) compared the plant compositions between the secondary forest and the original forest in 1936. And it never replanted on the land after the clear cutting in 1958. They just let the roots sprout and seeding there naturally. From March to September in 1968, they simply chopped off vines, weeds, and the invading intolerant tree species in the early successive stage, including *Aralia decaisneana*, *Rhus javanica var. roxburghiana*, *Litsea cubeba*, *Mallotus japonicus*, and excessive sprouts.

Experimental design

Liu *et al.* (1986) investigated the overstory and understory of the same area, and also

experimented on stand improvement in 1984. They utilized randomized blocks design in this area. They divided the area into four blocks as A to D, and assigned each block with three different experimental treatments. That came to a total of 12 plots, and each plot was 0.4 ha (40×100 m²). According to Lu and Sheu (1995), the investigation of broad-leaved forests in Taiwan should have a minimum plot of 500 m². The size of each sampling plot we used in our research met the requirements of sampling precision and ecological research. The attributes of plots were shown in Table 1. The target plant species reserved in each treatment group were described as below.

Treatment 1: main target species reserved included *Michelia compressa*, *Cinnamomum subvention*, *Schima superba*, *Machilus thunbergii*, *Cyclobalanopsis longinux*, *Cyclobalanopsis longinux* and *Castanopsis carlesii*. The stem density was 1,250 per hectare.

Treatment 2: main target species reserved included all Fagaceae plants, Lauraceae plants (cut the small trees, e.g. *Neolitsea* spp.), *Michelia compressa*, *Schima superba*, *Gordonia axillaris*, *Elaeocarpus sylvestris*, *Elaeocarpus japonicus*, *Cleyera japonica*, *Meliosma squamulata*, and *Engelhardtia roxburghiana*. The stem density was 2,000 per hectare.

Table 1. Attributes of plots of the broad-leaved secondary forest at Mt. Showchu in central Taiwan

Attributes of plot	Plot											
	A1	A2	A3	B1	B2	B3	C1	C2	C3	D1	D2	D3
Slope aspect (°)	95	95	95	30	30	30	10	10	10	163	163	163
Slope angle (°)	19	19	19	24	24	24	9	9	9	18	18	18
Altitude (m)	1,595	1,595	1,595	1,610	1,610	1,610	1,685	1,685	1,685	1,635	1,635	1,635
Treatment	1,250	2,000	control	1,250	2,000	control	1,250	2,000	control	1,250	2,000	control

Note: the numbers of treatment means the reserved individuals per hectare.

Treatment 3: control group. No treatment was done.

Data collection

Liu *et al.* (1986) pointed out that after more than three decades of succession, the compositions of secondary forests approximated to the climax of original forests. That showed that warm temperate broad-leaved forests after being chopped off in Taiwan even without forest tending could still regenerate to original vegetation compositions through sprouting and naturally seeding as long as on appropriate conditions. In the 12 plots of our experimental area, we obtained data from three periods: the time period before thinning treatments in 1983, that after the treatments in 1985, and eight years after the treatments in 1992. In order to understand the status of subsequent vegetation succession and regenerating processes, in the 12 plots with the above-mentioned treatments, we took another experiment in August of 1997, i.e. 13 years after thinning. We investigated all the trees over 5 cm in the diameter at breast height (DBH) for looking into the status of vegetation dynamics there.

Data analysis

The most widely applied statistical methods that ecologists used for researching species abundance models were negative binomial distribution in Pascal distribution and normal distribution. Specifically, they used methods closely related to negative binomial distribution, such as logarithmic series (logarithmic series distribution; log series distribution), broken stick model, and log normal distribution model. According to the species abundance models of species richness and number of individuals, researchers often drew a graph about the relative

importance of every species; with the X axis representing the level of individual number, and the Y axis representing the species richness or the relative importance of species richness. This kind of graph could be used to judge the structure of vegetation. It was commonly believed that four models, geometric series, logarithmic series, truncated log normal distribution and broken stick model, were ideal models (Whittaker, 1972; May, 1975; Whittaker, 1975; Whittaker, 1977; Southwood, 1978; Giller, 1984; Gray, 1987; Magurran, 1988). Therefore, we applied these four models on the data analysis. The process of statistical analysis and data testing methods were explained as below.

Geometric series

This was the distribution model of two-parameter. The vegetation structures in the early stage of succession often fit the species abundance model (Motomura, 1932; Whittaker, 1972; May, 1975; Pielou, 1975; Magurran, 1988). Through separately calculating the expectant number of individuals and the actual number of individuals in every species under the investigation, tested whether the data observed fit in with geometric series or not.

Logarithmic series

Fisher *et al.* (1943) used logarithmic series to describe the relationship between the number of species and the number of individuals because there were more rare species and fewer common species (i.e. dominant species). This was the distribution model of two-parameter (May, 1975). That was the expectant number of species from the number of individuals in each abundance class was calculated separately. And then the data were examined against the observed number of species

via χ^2 -test of goodness of fit to check if the result fit in with logarithmic series (Pielou, 1975; Magurran, 1988; Krebs, 1989; Hayek and Buzas, 1997). The α value of the logarithmic series could be found in nomograph for determining the α in Williams' studies (1947; 1964). And this value was proportional to the species richness. It could be regarded as a species richness index (Pielou, 1985; Magurran, 1988; Krebs, 1989; Hayek and Buzas, 1997).

Truncated log normal distribution

Based on Central Limit Theorem, Preston (1948) proposed the log normal distribution of two-parameter. However, Preston (1962) indicated that there were rarely data from ecological investigations with complete sampling. Often some of the rare species were ignored in the

sampling process. So the left side of the curved line in a log normal distribution was often saw the truncation. To solve this problem in the log normal distribution, Pielou (1975) applied the Maximum Likelihood Method, along with Cohen's (1959; 1961) auxiliary estimation function to develop a method for fitting the truncated log normal distribution. The current research applied the calculation procedure used by Slocomb *et al.* (1977), Magurran (1988), and Krebs (1989). The log normal diversity statistic (λ) could also be a species richness index. Furthermore, Slocomb *et al.* (1977) has changed the base of the log into 2. They revised the log normal distribution by using Maximum Likelihood Estimation, and applied the programming language of FORTRAN IV, to calculate the truncated log normal distribution step by step.

Table 2. χ^2 -test of goodness of fit for species abundance models at each plot of the broad-leaved secondary forest at Mt. Showchu in central Taiwan in 1983

Plot No.	χ^2 -test of goodness of fit			
	Geometric series	Logarithmic series	Truncated log normal distribution	Broken stick model
A1	0.0738	0.9229	0.9591	0.0971
B1	0.0000	0.1889	0.2303	0.0000
C1	0.0713	0.3280	0.4203	0.0060
D1	0.0066	0.0935	0.0432	0.0919
A2	0.0000	0.8378	0.8860	0.0000
B2	0.3042	0.0024	0.0072	0.0034
C2	0.3468	0.6356	0.2601	0.0013
D2	0.0000	0.9073	0.4667	0.0000
A3	0.0000	0.9856	0.9205	0.0000
B3	0.0000	0.3941	0.2775	0.0000
C3	0.9256	0.5753	0.8924	0.0466
D3	0.5606	0.1476	0.0281	0.0000

Note: The numbers in the table are probability values (p value), and the bold numbers indicate the best fit of the species abundance model for each plot.

Broken stick model

MacArthur (1957) proposed the broken stick model for one-parameter. The expectant species richness from the number of individuals in each abundance class was calculated separately. Then the data were examined against the observed species richness via χ^2 -test of goodness of fit to check whether the result fit in with the broken stick model or not (Webb, 1974; May, 1975; Magurran, 1988; Hayek and Buzas, 1997). Whittaker (1977), Thomas and Shattock (1986), and Magurran (1988) pointed out this model was different from the above two species abundance models. The geometric series showed a linear distribution, whereas the logarithmic series was often a curved distribution that approximated a linear distribution, and with a bigger slope. However, the broken stick model was a flatter

curved distribution. That meant it showed the majority were moderately abundant species.

The calculation of the above four species abundance models was based on the programming language of Visual Basic used by Tsai and Lu (2008) in their "Biodiversity Analysis System (BAS)". Then we applied a null hypothesis, H_0 : fitting the species abundance model. Just like Shi *et al.* (2000), Guo *et al.* (1995) tested the p value by using χ^2 -test of goodness of fit to judge whether our data fit the model or not.

RESULTS

Tests on geometric series

Motomura (1932) indicated the geometric series was based on ecological niche pre-emption hypothesis. When a certain dominant species took over the majority of resources and the

Table 3. χ^2 -test of goodness of fit for species abundance models at each plot of the broad-leaved secondary forest at Mt. Showchu in central Taiwan in 1985

Plot No.	χ^2 -test of goodness of fit			
	Geometric series	Logarithmic series	Truncated log normal distribution	Broken stick model
A1	0.0000	0.5374	0.2605	0.0000
B1	0.0000	0.2766	0.3649	0.0000
C1	0.0000	0.0995	0.0758	0.0000
D1	0.9686	0.1614	0.0447	0.0125
A2	0.0000	0.6211	0.8120	0.0000
B2	0.4925	0.1274	0.1980	0.0000
C2	0.2690	0.9380	0.6615	0.0000
D2	0.0073	0.8184	0.6455	0.0001
A3	0.0000	0.2461	0.1436	0.0000
B3	0.0000	0.7710	0.2565	0.0000
C3	0.9978	0.1718	0.0405	0.0086
D3	0.0013	0.4917	0.0660	0.0000

Note: The numbers in the table are probability values (p value), and the bold numbers indicate the best fit of the species abundance model for each plot.

subdominant species took over the rest of the resources, the individual number of each species distributed from the highest number to the lowest number. And the ecological niche occupied by each species was in accordance with k value in proportional parameter. This was mainly applied in research where there were fewer species, and where a single or very few environmental factors existed to dictate the community. Therefore, when the environment was severely polluted, species were in the early stage of the succession, there were few species and mostly dominant species, or the evenness was lower. we witnessed this kind of distribution model (Whittaker, 1972; May, 1975; Pielou, 1975; Southwood, 1978; Giller, 1984; Pielou, 1985; Gray, 1987; Magurran, 1988; Aoki, 1995; Hayek and Buzas, 1997).

From the χ^2 -test of goodness of fit for species abundance models in Tables 2, 3, 5, and 7, it showed that the fitness to the geometric series decreased at the 0.05 significance level in the following plots: A1 and C1 plots with treatment 1, B2 and C2 plots with treatment 2, C3 and D3 plots with treatment 3 in 1983 (before treatments); D1 plot with treatment 1, B2 and C2 plots with treatment 2, C3 plot with treatment 3 in 1985 (one year after treatments); C1 plot with treatment 1, C2 and D2 plots with treatment 2, D3 plot with treatment 3 in 1992 (eight years after treatments); D1 plot with treatment 1, C2 plot with treatment 2, and C3 plot with treatment 3 in 1997 (13 years after treatments). Furthermore, except B1 plot with treatment 1, A2 plot with treatment 2, A3 and B3 plots with treatment 3 that did not fit the geometric series in the all periods, there have been changes in other plots in the four periods. We deduced that besides chopping off trees, there were also other important factors, such as relative lighting and species compositions of different life-

forms that dictated the succession of the structures of vegetation.

Tests on logarithmic series

Fisher *et al.* (1943) conducted entomological research on the relationship between the species richness and the number of individuals within a small sample, and used the logarithmic series. This model was very close to the above geometric series, but there were few species, and most of them fit the geometric series given the condition that they were proportionally distributed in ecological niche. Moreover, if species were randomly distributed in ecological niche, the distribution of the species richness and number of individuals fit the logarithmic series (May, 1975).

From the χ^2 -test of goodness of fit for species abundance models in Tables 2, 3, 5, and 7, it revealed that it fit the logarithmic series at the 0.05 significance level in the following plots: A1, B1 and C1 plots with treatment 1, A2 and C2 plots with treatment 2, A3, C3 and D3 plots with treatment 3 in the all periods. All the plots with different thinning treatments in 1985 (one year after treatments) also fit the logarithmic series. But all plots in all years fit the logarithmic series at the significance level of 0.001. Besides, even if some plots did not fit the logarithmic series, α value could be regarded as effective species richness index for distinguishing different communities (Whittaker, 1972; Kempton and Taylor, 1976; Taylor, 1978; Kempton, 1979; Magurran, 1988; Hayek and Buzas, 1997). Moreover, the statistical software of SPSS 13.0 for Windows (SPSS Inc., 2004) was applied to conduct the univariate analysis of variance (UANOVA) in the general linear model (GLM) on the differences of α value in various time periods and for plots with various treatments, a Post Hoc Multiple Comparison with least-significant difference (LSD) test was done.

The results showed that there was no significant difference among various time periods ($p=0.555$), and different among various treatments ($p=0.004$). That was, treatment 1 was significantly different with treatment 2 ($p=0.019$) and treatment 3 ($p=0.001$), but treatment 2 and 3 had no significant difference ($p=0.320$). From Table 4 and 6, we derived that the higher the species richness was, the higher α value was, particularly in 1992 (8 years after treatments) and in 1997 (13 years after treatments). It indicated that this kind of communities had higher species richness.

Tests on truncated log normal distribution

The logarithmic normal distribution was suitable for vegetations that were bigger, more mature, highly differential, and in the later stage of succession which reached stability and equilibrium (May, 1975; Preston, 1980; Sugihara, 1980; Ugland and Gray, 1982; Gray, 1987; Magurran, 1988). However, since the

left side of the curved line in a logarithmic normal distribution was often truncated, most vegetations fit simultaneously the truncated log normal distribution and logarithmic series; that made it difficult for us to choose between the two models (Hughes, 1986; Magurran, 1988). Hayek and Buzas (1997) believed that the calculation of logarithmic series was simpler, and most vegetation fit this distribution model. Moreover, when rare species were the majority, or when there were small communities, they fit the logarithmic series (Kempton and Taylor, 1974; Taylor, 1978).

From the χ^2 -test of goodness of fit for species abundance models in Tables 2, 3, 5, and 7, it showed it fit the truncated log normal distribution at the 0.05 significance level in the following plots: A1, B1 and C1 plots with treatment 1, A2 plot with treatment 2, A3 and B3 plots with treatment 3 in the all periods. Furthermore, all plots in all years fit the truncated

Table 4. Species and sum of individuals at each plot of the broad-leaved secondary forest at Mt. Showchu in central Taiwan from 1983 to 1997

Plot No.	1983		1985		1992		1997	
	Species	Sum of individuals	Species	Sum of individuals	Species	Sum of individuals	Species	Sum of individuals
A1	30	579	28	421	33	551	32	565
B1	21	583	24	563	36	757	28	551
C1	12	500	21	525	35	968	23	498
D1	17	429	21	448	20	466	23	499
A2	35	522	33	445	34	534	43	511
B2	23	687	26	605	29	510	32	473
C2	24	704	27	682	27	681	24	656
D2	40	812	29	550	27	561	27	564
A3	36	1,305	37	1,009	40	999	33	711
B3	35	906	37	738	21	514	40	672
C3	29	753	31	538	26	524	32	740
D3	41	1,091	44	993	38	1,389	41	1,101

Table 5. χ^2 -test of goodness of fit for species abundance models at each plot of the broad-leaved secondary forest at Mt. Showchu in central Taiwan in 1992

Plot No.	χ^2 -test of goodness of fit			
	Geometric series	Logarithmic series	Truncated log normal distribution	Broken stick model
A1	0.0494	0.8636	0.3845	0.0001
B1	0.0000	0.4804	0.2696	0.0000
C1	0.7536	0.5831	0.1228	0.0000
D1	0.0010	0.2044	0.3890	0.8400
A2	0.0000	0.3860	0.7827	0.0000
B2	0.0002	0.1266	0.1954	0.0000
C2	0.8398	0.2432	0.3912	0.0005
D2	0.0647	0.0381	0.0273	0.0000
A3	0.0000	0.6354	0.7048	0.0000
B3	0.0000	0.0416	0.1110	0.0000
C3	0.0001	0.6979	0.4104	0.0005
D3	0.9404	0.4567	0.4983	0.0007

Note: The numbers in the table are probability values (p value), and the bold numbers indicate the best fit of the species abundance model for each plot.

log normal distribution at the significance level of 0.001. It revealed that this kind of vegetations was in the middle or later succession stage. Besides, we analyzed λ value of species richness index that Magurran (1988) figured out it could be used to discriminate the difference of various communities. When we conducted the univariate analysis of variance (UANOVA) in the general linear model (GLM) on the differences of λ value in various time periods and for plots with various treatments, a Post Hoc Multiple Comparison with least-significant difference (LSD) test was done. The results showed that there was no significant difference among various time periods ($p=0.493$), and different among various treatments ($p=0.003$). Otherwise, treatment 1 had significant difference compared with treatment 2 ($p=0.023$) and treatment 3 ($p=0.001$), but treatment 2 and 3 had

no significant difference ($p=0.218$). From Table 4 and 6, we derived that the higher the species richness was, the grater λ value was, particularly in 1992 (8 years after treatments) and in 1997 (13 years after treatments). It indicated that this kind of communities had higher species richness.

Tests on broken stick model

MacArthur (1957) proposed the broken stick model based on random niche boundary hypothesis. This model was appropriate to small and homogeneous taxa, and the sizes of inter-species were about the same. All species utilized equally the single restricted resource, and there was no overlap between any two species. Therefore, there was no dominant species, and the relative abundance was about fixed values and had higher evenness (King, 1964; Lloyd and Ghelard,

1964; May, 1975; Pielou, 1975; Whittaker, 1977; Southwood, 1978; Giller, 1984; Gray, 1987; Magurran, 1988; Cook and Graham, 1996; Baczkowski *et al.*, 1997).

Hayek and Buzas (1997) thought that very few communities would fit the broken stick model. From the χ^2 -test of goodness of fit for species abundance models in Tables 2, 3, 5, and 7, it showed that it did not fit the broken stick model at the 0.001 significance level in the following plots: B1 plot with treatment 1, D2 plot with treatment 2, A3, B3, and D3 plots with treatment 3 in the four periods. Furthermore, very few plots fit the broken stick model at the 0.05 significance level. Only A1 and D1 plots with treatment 1 in 1983 (before treatments) and D1 plot with treatment 1 in 1992 (eight years after treatments) fit the broken stick model. The results revealed that rare species and common species were fewer in these plots, which also had higher evenness.

DISCUSSION

Several researchers (Whittaker, 1972; Whittaker, 1975; Giller, 1984; Magurran, 1988) thought that communities in the early stage of succession process fit the geometric series, later fit the logarithmic series, and then fit the truncated log normal distribution. Furthermore, when the relative species abundance was at the fixed value, the majority of the homogenous community that was medium abundance species would fit the broken stick model. However, from Tables 2, 3, 5, and 7, most plots with treatment 1 in 1983 (before treatments) fit the truncated log normal distribution best, but only B1 plot fit the truncated log normal distribution best in 1985 (one year after treatments). All plots in 1992 (eight years after treatments) did not fit the truncated log normal distribution best, but D1 plot fit the broken stick model best. B1 and C1 plots in 1997 (13 years after treatments) fit the truncated log normal

Table 6. α and λ species richness indices at each plot of the broad-leaved secondary forest at Mt. Showchu in central Taiwan from 1983 to 1997

Plot No.	1983		1985		1992		1997	
	α	λ	α	λ	α	λ	α	λ
A1	7.120	48.298	7.215	41.126	8.192	48.082	7.818	46.212
B1	4.493	31.300	5.427	39.295	8.380	49.529	4.607	43.009
C1	2.334	15.566	4.633	28.654	7.558	44.114	5.309	37.948
D1	3.742	24.311	4.868	31.326	4.492	35.303	5.269	32.028
A2	9.000	55.312	8.781	52.882	8.600	60.559	11.950	74.279
B2	4.876	39.853	5.894	37.513	7.110	41.743	8.253	49.431
C2	5.068	31.154	5.949	35.712	5.941	39.245	5.189	37.484
D2	9.404	55.968	6.933	41.245	6.267	35.928	6.301	38.027
A3	7.280	47.165	7.981	50.179	8.816	54.854	7.580	48.222
B3	7.627	48.886	8.698	54.189	4.693	39.981	9.921	60.779
C3	6.339	42.725	7.611	45.372	6.122	36.592	7.209	45.231
D3	8.962	55.090	9.978	58.083	7.608	54.828	8.933	52.935

Table 7. χ^2 -test of goodness of fit for species abundance models at each plot of the broad-leaved secondary forest at Mt. Showchu in central Taiwan in 1997

Plot No.	χ^2 -test of goodness of fit			
	Geometric series	Logarithmic series	Truncated log normal distribution	Broken stick model
A1	0.0204	0.9033	0.4895	0.0003
B1	0.0000	0.3397	0.3880	0.0000
C1	0.0003	0.6812	0.8857	0.0000
D1	0.6093	0.0357	0.0026	0.0001
A2	0.0000	0.1904	0.0990	0.0152
B2	0.0000	0.9672	0.8088	0.0000
C2	0.9896	0.0759	0.0435	0.0009
D2	0.0000	0.9947	0.9003	0.0000
A3	0.0000	0.8914	0.8847	0.0000
B3	0.0000	0.8172	0.4931	0.0000
C3	0.9016	0.3188	0.2616	0.0010
D3	0.0001	0.9076	0.5870	0.0000

Note: The numbers in the table are probability values (p value), and the bold numbers indicate the best fit of the species abundance model for each plot.

distribution best. Furthermore, in the treatment 2, only A2 plot fit the truncated log normal distribution best in 1983 and 1985, A2 and B2 plots fit the truncated log normal distribution best in 1992, and most plots fit the logarithmic series best in 1997. Otherwise, the control groups with treatment 3 in 1983 did not fit the truncated log normal distribution best, but most control groups in 1985 fit the logarithmic series best. However, in 1992, A3 and B3 plots fit the truncated log normal distribution best, but in 1997, most of them fit the logarithmic series best.

The succession series of community is gradually changing and continuous. It is not as simple as the developmental stages as shown by the geometric series, logarithmic series, truncated log normal distribution, or broken stick model. Whittaker (1972; 1975) thought that communities

could fit the geometric series because of the appearance of dominant species in the later stage of succession. We may conclude that some plots belong to the later stage of the succession process especially B1 plot with treatment 1, A2 plot with treatment 2, A3 and B3 plots with treatment 3. This kind of plots appeared to be the climaxes that were mature and stable. Other plots went through structural changes in the succession process due to the competitions of inter-species. For example, it was predicted that D1 plot with treatment 1 in 1992 (eight years after treatments) would take over more ecological niche because of the natural replacement of the major dominant species.

CONCLUSIONS

Based on our research, we concluded that maybe the vegetation fit the various species

abundance models in the different succession series. Through data analysis in species abundance models, we gained some knowledge of dynamics in compositions of all the species in the succession. According to the results from our data analysis of the four models, we derived that no significant difference on the species richness indices for α and λ of broad-leaved secondary forests among the various time periods. Furthermore, in 1983 (before treatments) and in 1997 (13 years after treatments), the plots with the three treatments had minute dynamics in the structure of the vegetations. Most plots were in the middle and later stages of the succession, whereas other plots reached the climax. Otherwise, this study area is also an important habitat for the rare species, such as *Pasania nantoensis*, *Castanopsis eyrei*, *Symplocos decora* and *Eurya renegechiensis*. From our longitudinal investigations of the data analysis on the species abundance models, we are sure that the dynamics of the communities in terms of distribution of the species richness and the number of individuals in the evolutionary process. In hence, we strongly suggest it's necessary to re-monitoring the vegetation in the near future.

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LITERATURE CITED

- Aoki, I. (1995) Diversity and rank-abundance relationship concerning biotic compartments. *Ecol Model* 82: 21-26.
- Baczkowski, A. J., D. N. Joanes, and G. M. Shamia (1997) Properties of a generalized diversity index. *J Theor Biol* 188: 207-213.
- Chen, D. K., X. F. Zhou, and N. Zhu (1994) *Natural Secondary Forest: Structure, Function, Dynamic and Management*, 1st ed. Harbin: Northeast Forestry University Press. 586 p. [in Chinese].
- Cohen, A. C. J. (1959) Simplified estimators for the normal distribution when samples are singly censored or truncated. *Technometrics* 1: 217-237.
- Cohen, A. C. J. (1961) Tables for maximum likelihood estimates: singly truncated and singly censored samples. *Technometrics* 3: 535-541.
- Cook, L. M., and C. S. Graham (1996) Evenness and species number in some moth populations. *Biol J Linn Soc* 58: 75-84.
- Fisher, R. A., A. S. Corbet, and C. B. Williams (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *J Anim Ecol* 12: 42-58.
- Giller, P. S. (1984) *Community structure and the niche*, 1st ed. New York: Chapman and Hall. 176 p.
- Goan, L. H., and J. S. Chen (1995) *Third Forest Resources and Land Use Inventory in Taiwan*. Taipei: Taiwan Forestry Bureau. 258 p. [in Chinese].
- Gray, J. S. (1987) Species-abundance patterns. In: Gee, J. H. R., P. S. Giller, editors. *Organization of Communities, Past and Present*. Oxford: Blackwell Scientific Publications. p 53-67.
- Guo, X. G., B. H. Ye, Y. M. Gu, and Y. M. Chen (1995) Species-abundance distribution of

- gamasid mite community on small mammals in Western Yunnan, China. *Acta Parasitol Med Entomol Sin* 2(1): 56-61. [in Chinese with English summary].
- Hayek, L. C., and M. A. Buzas (1997) *Surveying Natural Populations*, 1st ed. New York: Columbia University Press. 563 p.
- Hughes, R. G. (1986) Theories and models of species abundance. *Am Nat* 128: 879-899.
- Kempton, R. A. (1979) The structure of species abundance and measurement of diversity. *Biometrics* 35: 307-322.
- Kempton, R. A., and L. R. Taylor (1974) Log-series and log-normal parameters as diversity determinants for the Lepidoptera. *J Anim Ecol* 43: 381-399.
- Kempton, R. A., and L. R. Taylor (1976) Models and statistics for species diversity. *Nature* 262: 818-820.
- King, C. E. (1964) Relative abundance of species and MacArthur's model. *Ecology* 45: 716-727.
- Krebs, C. J. (1989) *Ecological Methodology*, 1st ed. New York: Harper Collins. 654 p.
- Lin, C. D. (1956) Structure Investigation of the Secondary Forest on the Mt. Show-Chu in the Neng-Gau Forest Station [bachelor thesis]. Taichung: College of Agriculture. 56 p. [in Chinese].
- Liu, Y. C., U. C. Rin, C. H. Ou, and K. C. Lu (1986) Studies on the timber stand improvement of the secondary broad-leaved forest in the Hue-Sun Experimental Forest (I)- the plant community composition through 30-year succession after logging and primary treatment. *Q Jour Chin For* 19(3): 1-11. [in Chinese with English summary].
- Lloyd, M., and R. J. Ghelard (1964) A table for calculating the 'equitability' component of species diversity. *J Anim Ecol* 33: 217-255.
- Lu, K. C., and J. K. Sheu (1995) Study on the minimal area of sampling at broad-leaved forests in Taiwan. *J Expt Forest NCHU* 17(2): 13-58. [in Chinese with English summary].
- MacArthur, R. H. (1957) On the relative abundance of bird species. *Proc Nat Acad Sci* 43: 293-295.
- Magurran, A. E. (1988) *Ecological Diversity and Its Measurement*, 1st ed. Princeton: Princeton University Press. 179 p.
- May, R. M. (1975) Patterns of species abundance and diversity. In: Lody, M. L., J. M. Diamond, editors. *Ecology and Evolution of Communities*. Cambridge: Harvard University Press. p 81-120.
- Motomura, I. (1932) A statistical treatment of associations. *Jpn J Zool* 44:379-383.
- Pielou, E. C. (1975) *Ecological Diversity*, 1st ed. New York: John Wiley & Sons, Inc. 165 p.
- Pielou, E. C. (1985) *Mathematical Ecology*, 2nd ed. New York: Wiley-Interscience. 406 p.
- Preston, F. W. (1948) The commonness, and rarity, of species. *Ecology* 29: 254-283.
- Preston, F. W. (1962) The canonical distribution of commonness and rarity: part I. *Ecology* 58: 693-696.
- Preston, F. W. (1980) Noncanonical distribution of commonness and rarity. *Ecology* 61(1): 88-97.
- Shi, P. L., W. H. Li, J. X. Wang, and X. L. Liu (2000) Species-abundance relation of herb communities in subalpine timberline ecotone of Wolong Natural Reserve, Sichuan Province, China. *Acta Ecol Sin* 20(3): 384-9. [in Chinese with English summary].
- Slocumb, J., B. Stauffer, and K. L. Dickson (1977) On fitting the truncated lognormal

- distribution to species-abundance data using maximum likelihood estimation. *Ecology* 43(2): 185-215.
- Southwood, T. R. E. (1978) *Ecological Methods*, 2nd ed. London: Chapman and Hall. 524 p.
- SPSS Inc. (2004) *SPSS 13.0 for Windows*. USA: SPSS Inc.
- Sugihara, G. (1980) Minimal community structure: an explanation of species abundance patterns. *Am Nat* 116: 770-787.
- Taylor, L. R. (1978) Bates, Williams, Hutchinson-a variety of diversities. In: Mound, L. A., N. Warloff, editors. *Diversity of Insect Faunas: 9th Symposium of the Royal Entomological Society*. Oxford: Blackwell. p 1-18.
- Thomas, M. R., and R. C. Shattock (1986) Filamentous fungal associations in the phylloplane of *Lolium perenne*. *Trans Br Mycol Soc* 87(2): 255-268.
- Tsai, S. D., K. C. Lu, C. H. Ou, and M. Y. Lee (2000) Productivity and diversity analysis of the broad-leaved secondary forest at the Mt. Show-Chu in Hue-Sun Forest Station. *Q J For Res* 22(1): 51-62. [in Chinese with English summary].
- Tsai, S. T., and K. C. Lu (2008) *Biodiversity Analysis System*, 2nd ed. Yunlin: Transworld Institute of Technology. [in Chinese].
- Ugland, K. I., and J. S. Gray (1982) Lognormal distributions and the concept of community equilibrium. *Oikos* 39: 171-178.
- Webb, D. J. (1974) The statistics of relative abundance and diversity. *J Theor Biol* 43: 277-292.
- Whittaker, R. H. (1972) Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- Whittaker, R. H. (1975) *Communities and Ecosystems*, 2nd ed. New York: MacMillan Publishing. p 86-105.
- Whittaker, R. H. (1977) Evolution of species diversity in land communities. In: Hecht, M. K., W. C. Steere, B. Wallao, editors. *Evolutionary Biology Vol. 10*. New York: Plenum. p 1-67.
- Williams, C. B. (1947) The logarithmic series and the comparison of island floras. *Proc Linn Soc Lond* 158: 104-108.
- Williams, C. B. (1964) *Patterns in the Balance of Nature and Related Problems in Quantitative Ecology*, 1st ed. New York: Academic Press. p 324.
- Wu, B. H., Z. G. Liang, and D. Y. Jin (1991) *Management of Secondary Forest in Jilin Province*. Yanji: Publishing House of Yanbian University. 442 p. [in Chinese].