RELATIONSHIP BETWEEN SPECIES RICHNESS OF PLANT FUNCTIONAL GROUPS AND LANDSCAPE PATTERNS IN A TROPICAL FOREST OF HAINAN ISLAND, CHINA

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ZHANG ZD & ZANG RG. 2011. Relationship between species richness of plant functional groups and landscape patterns in a tropical forest of Hainan Island, China. The number of species and functional group (FG) classification were obtained from 135 grid sample plots (58 225 individuals) in a tropical forest landscape of Hainan Island, China in order to study the effects of landscape patterns of habitat types on species richness of woody plant FGs. Correlation between species richness and landscape pattern metrics were analysed by principal component and multiple linear regression analyses. The predominant determinants of species richness in different FGs were percentage of landscape, edge density (ED), total edge contrast index (TECI) and area-weighted mean shape index. The climax species were more sensitive to landscape fragmentation than the pioneer species in terms of species richness change. The species richness in the climax species increased markedly with increasing diversity and complexity of patches. In contrast, as ED and TECI increased, pioneer species slightly increased, but climax species and the total number of species decreased. This study further confirmed the prime role of landscape metrics in predicting the distribution of species richness in different FGs.

Keywords: Landscape fragmentation, pattern metrics, species diversity, natural forest, distribution, conservation

ZHANG ZD & ZANG RG. 2011. Hubungan antara kekayaan spesies kumpulan fungsi tumbuhan dengan corak landskap di dalam hutan tropika di Pulau Hainan, China. Bilangan spesies dan klasifikasi kumpulan fungsi (FG) diperoleh daripada plot sampel 135 grid (58 225 individu) di dalam landskap hutan tropika di Pulau Hainan, negara China. Kajian ini menyelidiki kesan corak landskap bagi jenis-jenis habitat terhadap kekayaan spesies FG tumbuhan berkayu. Korelasi antara kekayaan spesies dengan metrik corak landskap dianalisis menggunakan analisis komponen utama dan analisis regresi linear berbilang. Penentu utama kekayaan spesies dalam FG berlainan ialah peratusan landskap, kepadatan pinggir (ED), indeks jumlah kontras pinggir (TECI) dan purata indeks bentuk berasaskan luas. Dari segi perubahan kekayaan spesies, spesies klimaks lebih peka kepada pemecahan landskap daripada spesies perintis. Kekayaan spesies bagi spesies klimaks meningkat dengan ketara dengan peningkatan dalam diversiti dan kekompleksan tompok. Sebaliknya, apabila ED dan TECI bertambah spesies perintis bertambah dengan sedikit manakala spesies klimaks dan jumlah bilangan spesies berkurangan. Kajian ini selanjutnya mengesahkan peranan utama metrik landskap dalam meramal taburan kekayaan spesies dalam FG berlainan.

INTRODUCTION

Biodiversity conservation is gaining attention in recent decades with increasing public awareness and understanding of the relationship between biodiversity and species extinction (Hansen et al. 1991). There is a general consensus that landscapes are among the key drivers of the local dynamics of species and that landscape changes may be a threat to species diversity (Kerr et al. 2000). Biodiversity conservation can be realised by optimisation of habitat patches (Sala et al. 2000). Apparently, reconstruction of suitable habitat requires an in-depth understanding of landscape structure and the relationships between changes in landscape patterns, species composition and distribution.

At large spatial extents, the effects of landscape patterns on the richness and distribution of organisms can be explored based on landscape

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ecology approach (Fahrig 2003). The structure of a landscape mosaic is described by the spatial structure and configuration of patches, corridors and matrix called landscape elements (Gustafson 1998). A number of landscape metrics have helped us understand species richness patterns. For example, habitat diversity can explain species richness (Hannus & von Numers 2007). Landscape properties such as the size and heterogeneity of landscape are positively correlated with species richness (Hill & Curran 2003, Kadmon & Allouche 2007). Species richness is also frequently associated with isolation (Turner & Corlett 1996), shape (Honnay et al. 1999, Hernandez-Stefanoni 2006), and boundary characteristics (Fagan et al. 1999). The effect of landscape patterns on the number of species is important as it controls fundamental ecological processes such as speciation, dispersal and competition (Turner 1996). As a result of these processes, the fragmented forest landscape usually fails to support species assemblages found in intact, continuous forest.

Landscape patterns may be seen as environmental filters deleting species in particular conditions and through specific traits (Keddy 1992). Functional groups (FGs) are defined as groups of species either exhibiting similar responses to an environment or having similar effects on major ecosystem processes (Kelly & Bowler 2002). Due to differences in the ecological characteristics and requirements, different FGs could have different responses to landscape change. For example, the regeneration of large-seeded trees is seriously affected by the landscape fragmentation (Harrington et al. 1997). Habitats that are more isolated are inaccessible to species of low dispersal ability (Matlack 1994). The FG approach has shed new light in the exploration of the impact of landscape fragmentation on biodiversity. It is possible to study changes in habitats of a particular FG and determine whether or not the habitats are too fragmented for the FG to survive.

We evaluated variables of landscape patterns of habitat types that were most closely related to species richness of woody plant FGs. We tested landscape metrics linked to landscape composition (patch type area) and landscape configuration (fragmentation, shape irregularity and contrast), some of them rarely analysed in the past despite their potential interest in this context. It is initially expected that variables related to fragmentation will have a significant impact on species richness and the relationship whether positive or negative depends on specified FG considered.

Hainan Island is located in the southern most part of China, where tropical forests are distributed on the northern edge of the tropical Asia and are recognised as one of the forest ecosystems with the highest biodiversity in China. Due to extensive deforestation and long-term intensive agricultural landuse, the area of primary forests has been greatly reduced, resulting in landscape mosaics of a few old-growth forest patches dispersed in the large matrix of degraded ecosystems of various recovery stages. Obviously, fragmentation of landscape has certainly affected biodiversity of this island. In order to conserve biodiversity and properly manage the tropical forest, it is important to understand the relationship between landscape pattern changes and biodiversity. Here we report a study in the Bawangling forest area on Hainan Island, China. This study was aimed at providing further insights into the understanding of woody plant species richness patterns based on FG from a landscape ecology perspective. We hypothesise that (1) factors related to area, shape, isolation and contrast will have a significant impact on species richness patterns and that (2) climax species are more sensitive to landscape pattern changes than pioneer species due to differences in the ecological characteristics. The results of this study will be helpful to conserve biodiversity in fragmented tropical forest landscape.

MATERIALS AND METHODS

Study area

The study area is located in the Bawangling forest region (18° 53' N, 109° 53' E), Hainan Island, south China. The size of the area is about 480 km^2. The majority of this area is mountainous with altitude from about 50 to 1654 m asl. It has typical tropical monsoon climate, with distinct dry season (December till April) and wet season (May till November). The annual mean temperature and precipitation are 24.2 °C and 1677.1 mm respectively. Soils at higher elevations in the area are a complex of red loam and yellow loam, while latosol developed from granite dominates soils at lower elevations. The predominant vegetation types are the tropical lowland rainforest, montane rainforest, montane evergreen forest, montane dwarf forest and coniferous forest, among which the tropical lowland rainforest and montane rainforest are widespread. Although some primary vegetation types are preserved to a certain extent in the mountains (Zang et al. 2004), most areas in Bawangling has experienced slash-and-burn agriculture and commercial logging which destroyed most of the primary forest. Since 1994, timber harvest has been banned in Hainan Island. Thus, Bawangling rainforest is naturally recovering.

From March till September 2005, we surveyed the forest vegetation area in Bawangling. The core area of Bawangling is composed of five continuous landscapes (Figure 1). The size of each landscape is between 71.72 (landscape 1) and 89.51 km^2 (landscape 5). Sample plots were investigated systematically. The study area was divided into 1 × 1 or 2 × 1 km grid. Each grid cross-point was set as the centre of a sample plot where species within 20 × 20 m^2 were recorded. Inaccessible grid cross-points were sampled from nearby area. As such, we surveyed a total of 135 natural forest sample sites (Figure 1). Within each sample plot, all free standing woody stems with diameter at breast height (dbh) ≥ 1 cm were counted, measured and identified to the species level. Determination of the time since the last disturbance and of the disturbance type on each sample plot was made on the basis of timber harvest archives of the Forestry Bureau of Bawangling. In addition, we conducted interviews with experienced loggers for harvesting operations. The exact location of each sample site was obtained with global positioning system (GPS).

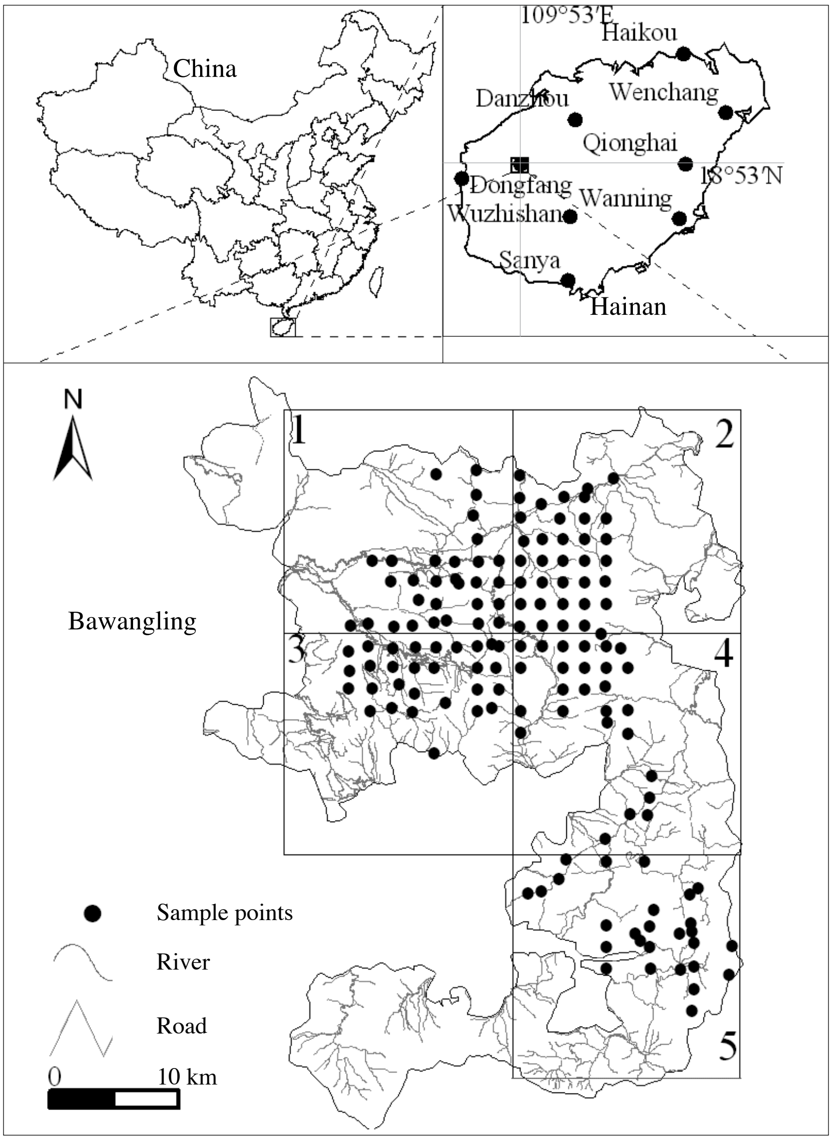

Figure 1 Location of the sample plots in the studied area. 1–5 = landscape 1–landscape 5

Functional group classification

In this area, there were 579 plant species that belonged to 82 families and 247 genera. A total number of 58 225 individuals of woody plant species were recorded. We classified species into FGs based on their successional status and potential maximum height according to Köhler et al. (2000). The successional status of a species was classified as either pioneer or climax. The determination of the successional status of a species is mainly based on seed size and wood density (Zhang et al. 2008). The species with small seeds, large seed mass and light wood density were grouped together for pioneers and species with heavy wood and large seeds for climax species. Trees were classified into shrub (2–5 m), subcanopy (5–15 m) and canopy (> 15 m). FGs were then categorised as pioneer shrub (F1), pioneer subcanopy tree (F2), pioneer canopy tree (F3), climax shrub (F4), climax subcanopy tree (F5) and climax canopy tree (F6). In each natural forest sample plot, the total number of species and number of species in each FG were counted.

Calculation of landscape pattern metrics

Patch type was classified based on a cloudless Landsat thematic mapper (TM) image and field survey data. The georeferenced image data were geometrically rectified following 5 × 5 low-pass filtering. A supervised classification technique was run. Nine patch types were distinguished: tropical forests of four recovery stages: < 10 years (I), 11–20 years (II), 21–35 years (III), and ≥ 36 years (IV), shrub grassland (GR), pine plantation (MP), plantation of broadleaved trees (MB), water (WA) and others (OT). The overall classification accuracy of our image was 76.2%, similar to that (73.0%) reported by Espírito-Santo et al. (2005). Lucas et al. (2000) reported an accuracy of less than 60%. Comparing with previous reports, our classification accuracy is acceptable.

Landscape metrics were calculated with Fragstats 3.3 (McGarigal et al. 2002). Since this study dealt with the relationship between natural vegetation landscape patterns and species richness, natural vegetation patches were the concern of the calculation and other patches (MP, MB, WA and OT) were used as 'background'. Landscape pattern metrics involved three spatial levels: landscape, patch and class. In the current calculation, class (patch type) was used as the basic unit, i.e. all the individual patches of the same vegetation class. The landscape pattern metrics based on patch type were calculated separately for each of the five continuous landscapes.

Since several indices at patch type level were similar (Hargis et al. 1998), we considered the basis of the frequency of their use in the landscape ecology literature (Mazerolle & Villard 1999) and different aspects of the patch type configuration (Hernandez-Stefanoni 2006) during indices selection. The selected factors related to both landscape composition and configuration may explain the plant diversity in the tropical forests of the study area. The selected metrics were area/density/edge (percentage of landscape—PLAND, patch density—PD and edge density—ED), shape (area-weighted mean shape index—SHAPE_AM), isolation/proximity (mean area-weighted similarity index—SIMI_AM) and contrast (total edge contrast index—TECI). A description of each metric is given in Table 1.

The calculation of SIMI_AM requires the determination of search radius and similarity weights between patch types. This study applied 10 pixels (300 m) as the search radius. The similarity weights were determined by divergence between patch types as described by Chang et al. (2004) (Table 2). The weighted contrast index was indicated as the inverse values of similarity weights for the calculation of TECI.

Statistical analyses

The total number of species and species richness in each FG were calculated as the mean of all sample plots inside the same patch type. Pearson correlation coefficients between each pair of landscape–pattern metrics, as well as the correlation of these metrics with the number of species of FGs were computed. In order to avoid highly multicolinearity problem that often emerged among landscape metrics and obtain independent variables, we also performed principal component analysis for the six metrics of classes using varimax rotation procedure. We performed a multiple regression analysis for the total number of species and the species richness in each FG against the final principal components created from landscape metrics of patch types. The variables were transformed with $\log_{10}(x + 1)$

Table 1 Description of metrics used to quantify landscape spatial patterns of individual patches

Type of metric/code	Metric	Description
Area/density/edge		
PLAND	Percentage of landscape	This metric is calculated as the sum of the areas (m^2) of all patches of the corresponding patch type, divided by the total landscape area (m^2). It is a measure of landscape composition, specifically, how much of the landscape consisted of a particular patch type (natural vegetation class).
PD	Patch density	This metric measures the number of patches of the corresponding patch type divided by total landscape area.
ED	Edge density	This index is a measure of total edge length of each patch type on a per unit area basis that facilitates comparisons among patch types of varying sizes.
Shape		
SHAPE_AM	Area-weighted mean shape index	This metric is a measure of shape complexity of a patch compared with a standard shape of the same size. Here it was measured as the weighted mean area of the shape indices of the patches corresponding to a patch type.
Isolation/proximity		
SIMI_AM	Mean area-weighted similarity index	This metric quantifies the spatial context of a patch in relation to its neighbours of the same or similar class. Here it was measured as the mean of the similarity indices of the patches corresponding to a patch type.
Contrast		
TECI	Total edge contrast index	This metric is the sum of the lengths (m) of each edge segment involving the corresponding patch type multiplied by the corresponding contrast weight, divided by the sum of the lengths (m) of all edge segments involving the same type. High values of this index mean that the edge present is of high contrast and vice versa. The weighted edge contrast between vegetation classes demanded to compute this metrics was calculated as the inverse values of the similarity weights.

Source: McGarigal et al. (2002)

Table 2 Similarity weight values between pairs of patch types

	GR	I	II	III	IV
GR	1	0.46	0.17	0.15	0.07
I		1	0.75	0.62	0.50
II			1	0.87	0.75
III				1	0.87
IV					1

GR = shrub grassland; I, II, III, IV refer to tropical forests of four recovery stages: < 10 years, 11–20 years, 21–35 years and ≥ 36 years respectively

as necessary to meet the requirements of linearity and normal distribution (Legendre & Legendre 1998). The transformed data proved to meet the requirement of normality through performing Kolmogorov Smirnov test.

RESULTS AND DISCUSSION

The mean species richness in each FG within each patch type is presented in Figure 2. In general, as the time of recovery increased, the number of species of climax FGs (F4, F5, F6) increased gradually. However, the greatest number of species for the above classes did not appear in the patch type IV. Instead, it appeared in the secondary patch type III that had 21–35 years of recovery. The number of species in the pioneer FGs (F1, F2, F3) decreased slightly with the progress of recovery.

Correlation analysis (Table 3) demonstrated that five pairs of landscape indices were positively correlated ($p < 0.05$) and two pairs, negatively correlated ($p < 0.05$) among 15 paired combinations of the metrics of patch types. This indicated a degree of redundancy in terms of the information that landscape metrics provided.

Considering the correlation of the number of species of the different groups with the landscape metrics of classes, the results varied depending on different landscape metrics and FGs considered. PLAND was positively correlated with the number of species of the late succession stage FGs (F5 and F6) ($p < 0.01$) with $r > 0.5$, but it had limited influence on the pioneer FGs (F1, F2 and F3)

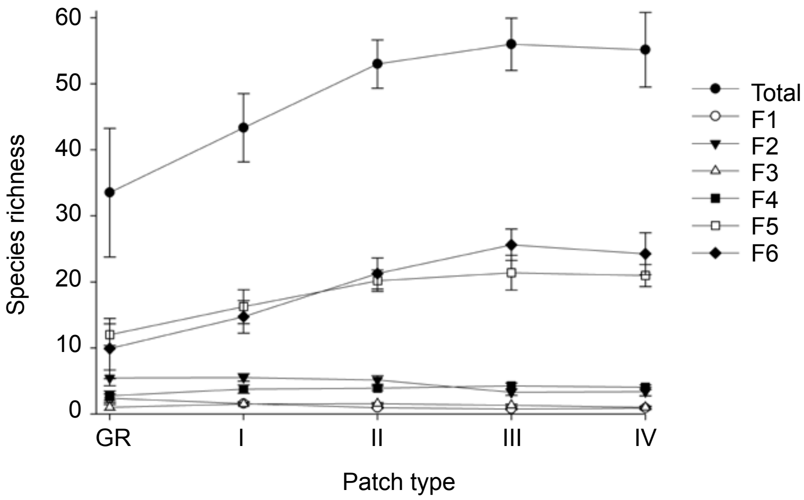

Figure 2 Means and standard errors of woody plant richness among patch types in Bawangling, Hainan Island, China. GR = shrub grassland; I, II, III, IV refer to tropical forests of four recovery stages: < 10 years, 11–20 years, 21–35 years and ≥ 36 years respectively; F1 = pioneer shrub, F2 = pioneer subcanopy tree, F3 = pioneer canopy tree, F4 = climax shrub, F5 = climax subcanopy tree, F6 = climax canopy tree

Table 3 Pearson correlation coefficients between metrics of patch types and between species richness of different functional groups or the total number of species and landscape patterns of patch types

Variable	PLAND	PD	ED	SHAPE_AM	SIMI_AM	TECI
PLAND						
PD	0.332					
ED	0.676**	0.449*				
SHAPE_AM	0.496**	0.016	0.472*			
SIMI_AM	0.385	-0.351	0.271	0.570**		
TECI	-0.541**	-0.472*	0.403	0.340	-0.289	
Total	0.581**	0.236	-0.566**	0.534**	0.340	-0.607**
F1	0.326	0.248	0.466*	0.450*	0.382	0.521*
F2	0.470*	0.098	0.459*	0.592**	0.379	0.771**
F3	0.264	0.047	-0.424*	0.640**	0.013	0.485*
F4	0.462*	0.214	-0.583**	0.342	0.456*	-0.597**
F5	0.652**	0.219	-0.539**	0.492**	0.350	-0.529**
F6	0.559**	0.162	-0.525**	0.507**	0.391	-0.674**

** $p < 0.01$, * $p < 0.05$; F1 = pioneer shrub, F2 = pioneer subcanopy tree, F3 = pioneer canopy tree, F4 = climax shrub, F5 = climax subcanopy tree, F6 = climax canopy tree; See Table 1 for definitions of patch-type metrics.

and climax shrub FG F4 with r ranging from 0.264 to 0.470. ED and TECI were negatively correlated with the number of species of climax FGs ($p < 0.01$). However, ED had a relatively weak influence on the pioneer FGs. SHAPE_AM was also significantly associated with most of the FGs and the correlations were positive (Table 3). Contrary to the above landscape metrics, PD and SIMI_AM were not significantly related to species richness of most of the FGs ($p > 0.05$).

Through principal component analysis, two components with eigenvalues greater than one were selected as meaningful factors, which explained 80.1% of the total variation. The first principal component explained 53.7% of the total variation. It was composed of PLAND, PD, ED and TECI, reflecting the changes in patch size, density, edge and contrast. The second principal component, which explained 26.4% of the total variation, reflected the characteristics of patch shape (SHAPE_AM) and proximity (SIMI_AM) (Table 4).

Regression models for the two principal components were established after multiple regression analysis (Table 5). The first component contributed much greater than the second to the models especially in predicting the total number of species and species richness of climax FGs. This result demonstrated that accompanying the increase in patch size and the decrease in patch density, edge density and contrast, the total number of species and species richness of all FGs increased. The second component, reflecting SHAPE_AM and SIMI_AM, varied depending on the different FGs concerned in the ability to predict species richness. In general, the more irregular a patch and the similarity of a patch to its neighbours, the greater the number of species and species richness of FGs within this patch type.

Forest fragmentation changes landscape functions as well as alters the behaviour and dynamics of plant populations (Bierregaard et al. 2001). Marked variation in plant community composition and species distribution as a function of degree of fragmentation is well documented

Table 4 Principal component analysis factor scores on the two derived principal component axes after a varimax rotation

Variable	Component	
	PC1	PC2
PLAND	0.930	0.313
PD	-0.754	-0.154
ED	-0.726	-0.358
SHAPE_AM	0.196	0.846
SIMI_AM	0.086	0.866
TECI	-0.881	-0.550

PLAND = % of landscape, PD = patch density, ED = edge density, SHAPE_AM = area-weighted mean shape index, SIMI_AM = mean area-weighted similarity index, TECI = total edge contrast index; PC = principal component

Table 5 Multiple regression analysis between species richness of functional groups and patch-type metrics

Dependent variable	Intercept	Model parameter	B	t-value	p	r^2
Total	57.927	PC1	13.227	6.295	0.000	0.681
		PC2	5.127	3.012	0.005	
F1	1.372	PC1	4.252	2.950	0.008	0.397
		PC2	0.567	1.954	0.066	
F2	4.578	PC1	1.288	2.162	0.02	0.443
		PC2	0.837	2.038	0.057	
F3	11.353	PC1	3.482	2.484	0.019	0.586
		PC2	4.753	2.982	0.006	
F4	4.770	PC1	5.855	3.291	0.002	0.609
		PC2	0.860	1.814	0.075	
F5	21.896	PC1	5.162	4.690	0.000	0.545
		PC2	0.938	2.077	0.037	
F6	23.958	PC1	8.362	5.999	0.000	0.656
		PC2	0.476	0.414	0.684	

F1 = pioneer shrub, F2 = pioneer subcanopy tree, F3 = pioneer canopy tree, F4 = climax shrub, F5 = climax subcanopy tree, F6 = climax canopy tree

(Holt et al. 1995). In tropical rainforest, some quantitative measures of habitat fragmentation such as area, edge matrix, distance and the combined effects drive the evolution of species distribution (Laurance & Vasconcelos 2004). We have demonstrated that the major parameters affecting the species richness of different FGs are PLAND, ED, SHAPE_AM and TECI. This is consistent with the findings of Hernandez-Stefanoni (2006) who analysed the relationship between fragmentation and species richness of shrubs and trees. PLAND, a measure of landscape composition, is positively correlated with species richness in most of the FGs. This may indicate the importance of fragmentation and diversity of habitats on species richness when the effect of area of a fragment on species richness is weak. That is to say, a certain level of disturbance will not decrease biodiversity. On the contrary, the resulting increase in habitat diversity has positive effects on the species richness of most of the FGs. Previous studies have shown that two geographically isolated forest patches have more diverse habitat than a single large patch of the same size (Zacharias & Brandes 1990). The number of species in several small spread habitat patches is usually greater than that in a large single forest patch of the combined size (Honnay et al. 1999). It, therefore, clearly indicates that the availability of different resources may be important for the establishment of plant species. Similarly, the availability of landscape resources, to a certain extent, affects species establishment and distribution (Hernandez-Stefanoni 2006).

In addition to PLAND, SHAPE_AM was also positively correlated with species richness in most FGs (Table 3). That is to say, the more irregular is the shape of a patch, the more diverse the species in that habitat. Similar result was also found by Honnay et al. (1999). The characteristics of habitat shape have been shown to influence inter-patch processes such as animal migration, woody plant colonisation, and the transfer of matter and energy (McGarigal & Marks 1995). Irregularly-shaped patches are beneficial to the above process and thus maintain a higher biodiversity. Edge density and TECI were negatively related to species richness in most FGs. The greater value of ED indicates greater fragmentation, suggesting greater human intervention such as extensive logging. Total edge contrast index reflects the degree of similarity of patch to its neighbours. High-contrast edges as a barrier may inhibit some animals from seeking supplementary resources in surrounding patches and further passively impact the dispersion patterns of animal-dispersed species (McGarigal & Marks 1995). Besides, biodiversity within a patch depends not only on the conditions within the patch, but an adjacent patch can provide seed sources and suitable microclimate (Zonneveld 1995). The results from principal component analysis and multiple regression analysis showed that in addition to the influence of a single index of landscape, the combined effects of multiple indices also determined the species richness in a habitat (Tables 4 and 5).

Species richness in a given patch type is determined not only by landscape patterns but also by the functional characteristics of different FGs (Metzger 2000). Ecological and life-history differences between pioneer and climax species often cause great variations in responses to habitat fragmentation. Pioneer species typically have a series of correlated traits, including high fecundity capacity, long dispersal, small seed size, great seed number and rapid growth when resources are abundant (Rees et al. 2001). These characteristics promote the dispersion of pioneer species and enhance the ability of species to access the fragmented landscapes. In addition, the rapidly growing ability allows them control over a given patch, especially those that have been seriously disturbed (Whitmore 1989). These functional characteristics determine that pioneer species are less susceptible to landscape fragmentation and even increase the number of species in forest boundaries. This view was reflected by the fact that pioneer species had weak correlation with PLAND and high or significantly positive correlation with ED and TECI (Table 3). On the contrary, the climax species usually have low reproductive rate and large animal-dispersed seeds (Chazdon et al. 2003). Researchers have discovered that area close to maternal trees is usually characterised by greater number of climax species seedlings. However, climax species are less likely to spread to newly formed patches because of their strong dependence on animal dispersers. The activity of seed-dispersing animals is usually affected by landscape fragmentation such as size of a fragment, edge effects on forest structure and floristics, quality of the matrix, and disturbances such as hunting and wood gathering (Alvarez-Buylla & Martinez-Ramos 1992). The decrease in species richness of a patch is likely the result of decrease in (even the disappearance of) activities of seed-dispersing animals (Hansson & Angelstam 1991). As stated above, climax species are more susceptible to landscape fragmentation and especially responsive to PLAND, ED and TECI (Table 3). Simultaneously, these results have also shown that native dominant species or FGs comparing with invading or pioneer species are more vulnerable to landscape fragmentation and more prone to extinction.

The above analysis demonstrated that landscape patterns and the characteristics of FGs significantly affected the dispersion of species among habitats. The study also showed that shrub species were less sensitive than trees to landscape fragmentation. This result may be determined by two reasons. Shrub species are small in number within study area. This may partly result in shrub response being statistically insignificant to fragmentation. The other factors that contributed to shrub distribution may be the local habitat condition, competitive interactions, intensity, and type of human disturbance and microclimate conditions, which determined the success of colonisation of shrub and also other FGs (Metzger 2000, Potts et al. 2002). The current study explored the relationship between landscape patterns and the species richness of woody plants in different FGs at the patch level. More detailed studies are needed to understand the biodiversity dynamics in the landscape scale.

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