Functional diversity increases with species diversity along successional gradient in a secondary tropical lowland rainforest

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Abstract: Functional diversity (FD) is a good predictor of ecosystem multi-functionality. Few empirical studies have been conducted on the patterns of variation in functional diversity during secondary succession in tropical forests. In this paper, we measured six functional traits for woody plants and tried to understand how functional and species diversity change along a chronosequence on Hainan Island, South China. The results showed that both species and functional diversity increased gradually during secondary succession, they increased significantly after 30 years of stand recovery. Functional diversity could be well predicted by species diversity within each successional stage. A sigmoid logistic relationship between functional diversity and species diversity existed when all the successional stages were combined. Our results suggest that species diversity is a good predictor of functional diversity and functional redundancy exists during the early and late successional stages.

Resumen: La diversidad funcional es un buen predictor delamultifuncionalidad del ecosistema. Se han realizado pocos estudios empíricos sobre los patrones de variación en la diversidad funcional durante la sucesión secundaria en bosques tropicales. En este trabajo medimos seis atributos funcionales de plantas leñosas y tratamos de entender cómo cambianla diversidad funcional y la de especies en una cronosecuencia en la isla de Hainan, sur de China. Los resultados mostraron que tanto la diversidad funcional como la de especies aumentaron gradualmente durante la sucesión secundaria, y que aumentaron significativamente después de 30 años de recuperación delosrodales. La diversidad funcional podría ser predichacorrectamente por la diversidad de especies en cada etapa sucesional. Se observó una relación sigmoide logística entre la diversidad funcional y la diversidad de especies al combinar todas las etapas sucesionales. Nuestros resultados sugieren que la diversidad de especies es un buen predictor de la diversidad funcional y que hay redundancia funcional durante las etapas tempranas y tardías de la sucesión.

Resumo: A diversidade funcional (FD) é um bom preditor damulti-funcionalidadedo ecossistema. Poucos estudos empíricos têm sido realizados sobre os padrões de variação na diversidade funcional durante a sucessão secundária em florestas tropicais. Neste artigo, mediram-se seis características funcionais para plantas lenhosas, e tentou-se compreender como a diversidade funcional e específica ao longo de umasequência cronológica na ilha de Hainan, sul da China. Os resultados mostraram que quer as espécies quera diversidade funcional aumentaram gradualmente durante a sucessão secundária, de forma significativa após 30 anos de recuperação da parcela. A diversidade funcional pode ser bem preditapela diversidade dasespécies dentro de cada estágio da sucessão. A relação logística sigmoide entre a diversidade

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funcional e a diversidade de espécies existia quando todos os estágios sucessão foram combinados. Os nossos resultados sugerem que a diversidade de espécies é um bom proditor da diversidade funcional existindo redundância funcional durante os estágios sucessionais precoces e tardias.

Introduction

The potential effects of biodiversity loss on ecosystem functioning and services have been a primary concern of ecologists during the last decade (Hooper *et al.* 2005; Sasaki *et al.* 2009). Functional diversity (FD), the value and range of functional traits of the organisms present in a given ecosystem (Díaz & Cabido 2001; Díaz *et al.* 2007), has a significantly important effect on ecosystem processes (Klumpp & Soussana 2009; Falster *et al.* 2011) as well as it is one of the best predictors of ecosystem functioning (Griffin *et al.* 2009; Petchey & Gaston 2006).

Studies related with 'functional diversity' have been increasing rapidly, especially in the last decade (Cadotte 2011). However, few empirical studies have been designed to assess how functional diversity varies across environmental and successional gradients in forests. Although the relationship between functional diversity and species diversity (FD-SD) remains poorly understood for nearly all ecosystem types (Bihn *et al.* 2010; Naeem 2002), it is critically important to determine this relationship for developing both a mechanistic understanding of community assembly and appropriate approaches to protecting and restoring biological communities (Micheli & Halpern 2005). FD-SD can be used to explore to what extent functional diversity is complementary among species or whether functional redundancy among species exists (Lohbeck *et al.* 2011; Petchey & Gaston 2002). A positive linear relationship of FD-SD indicates that each species has a relatively unique trait; a logarithmic FD-SD relationship suggests that functional diversity may increase rapidly at lower diversity levels and subsequently increases at a declining rate as functional redundancy increases; a sigmoid logistic FD-SD relationship depicts two-phase functional redundancy, functional redundancy at low levels of species diversity followed by a rapid increase at

intermediate levels, until functional diversity reaches an asymptote at high levels (Micheli & Halpern 2005; Sasaki *et al.* 2009).

Functional diversity has an important effect on ecosystem functioning through functional traits (Lavorel & Grigulis 2012; Ruiz-Jaen & Potvin 2011). The increase of functional diversity with species diversity implies that ecosystem functioning would improve with the rise of species diversity. In addition, functional redundancy rather than functional diversity can improve ecological resilience of ecosystem, which is tightly related to the maintenance or recovery of ecosystem functioning under changing environmental conditions or disturbance events (Flynn *et al.* 2009; Laliberte *et al.* 2010). Moreover, with functional redundancy, ecological functions can be safeguarded against species loss (Bihn *et al.* 2010).

The concept of functional redundancy is at the core of the theory relating changes in ecosystem functioning to species loss (Sasaki *et al.* 2009). Low ecological redundancy implies that functional traits are rapidly lost from a system as diversity declines. In contrast, high redundancy would indicate that ecosystem functions are robust to changes in diversity, possibly along the trajectory of both degradation and recovery.

In this paper, we tried to understand how functional and species diversity change during tropical forest succession on Hainan Island, China. Our aim was to increase the knowledge of functional change in the process of vegetation recovery through empirical investigations. All the tree and shrub species (including 6,663 individuals of 274 species) were sampled in 200 plots with a well recorded history of shifting cultivation. Six functional traits that are important for plant performance and ecosystem processes were measured for woody plants. The relationship between functional diversity and species diversity during secondary forest succession was specifically explored. We hypothesized that: (1) species and functional

diversity should increase with tropical forest succession; (2) species diversity could predict functional diversity within each successional stage; and (3) functional redundancy would exist during succession.

Materials and methods

Study sites

This study was conducted in the Bawangling Forest Region (BFR, 18° 52′-19° 12′ N, 108° 53′-109° 20′ E) on Hainan Island, south China. It is at the northern edge of Asian tropical forest (Ding *et al.* 2012). The BFR is ca 500 km², with an elevation range of 100 - 1654 m asl. This study was conducted in the tropical lowland rainforest which is found at elevations below 800 m. The mean annual temperature is 23.6 °C, and annual precipitation is 1,677 mm, with a distinct wet season from May to October and a dry season from November to April.

Before 1994, tropical forests on Hainan Island have experienced extensive deforestation by logging and shifting cultivation. The deforestation rate in this area is higher than the average deforestation rate of the world, due to the shortage of timbers and agricultural lands (Zang *et al.* 2004). Most of primary lowland tropical forests in low-elevation areas of Hainan Island have been converted to shifting cultivation lands. After a relative short period of cultivation, the lands were usually abandoned due to soil erosion, and natural recovery of vegetation began. Consequently, secondary forests of different recovery degrees or successional stages can be found in the low-elevation areas of Hainan Island, which affords a good site to study secondary forest succession by using a space for time substitution approach.

The field investigation was conducted on plant community in different stages of succession. Forest which had recovered 18 years after shifting cultivation (18-year-old fallow) was considered as locating in the first stage of succession. Forest which had recovered 30 years after shifting cultivation (30-year-old fallow) was considered as locating in the second stage of succession. Forest which had recovered 60 years after shifting cultivation (60-year-old fallow) was considered as locating in the third stage of succession. Old-growth forest which was not subjected to anthropological disturbance was considered as locating in the last stage of succession. 50 plots (20 m × 20 m) were sampled randomly in every stage

of succession and a map with location of plots is given in Fig.1. Information on the history of land use of the plots was obtained from management records of Bawangling Bureau of Forestry of Hainan. These plots have similar topographic conditions. They are located in low hills with slopes of about 15 degrees, and their elevations range from 412 - 626 m asl.

Species and traits

Field sampling was conducted in these plots of lowland tropical forests from May to July in 2011. All trees and shrubs with diameter at breast height (dbh) ≥1 cm in each plot were identified and measured. Species names were recorded in accordance with Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China 2004). All species were sampled to measure functional traits data. For rare species (< 10 individuals per ha), all individuals were sampled and over ten individuals per common species (≥ 10 individuals per ha) were sampled. Totally, 6,663 individuals of 274 species were measured. For each individual, two to five recently-expanded leaves, including petioles and rachises of compound leaves were collected (Cornelissen *et al.* 2003). Leaf surface area was measured with a leaf area meter (LI-COR 3100C Area Meter, LI-COR, USA). Leaf thickness (LT, mm) was measured for each lamina as the mean of three measurements using a Mitutoyo digital micrometer (Mitutoyo Instruments, Singapore). Leaf total chlorophyll content (CC) was estimated using three values per lamina from a SPAD 502 Plus meter (Konica Minolta, Japan). Laminar dry mass was measured by drying to constant mass at 60 °C (around 72 h), and specific leaf area (SLA, cm² g⁻¹) was calculated for each lamina as the ratio of leaf surface area to leaf mass. Leaf dry matter content (LDMC, g g⁻¹) was the oven-dry mass divided by its fresh mass. Leaf tissue density (LTD, g cm⁻³) was calculated as leaf mass per leaf area divided by leaf thickness (Baraloto *et al.* 2010; Holdaway *et al.* 2011).

To characterize species wood density (WD, g cm⁻³), which is more laborious, we sampled branches (1 cm ≤ diameter ≤ 2 cm) from one to ten individuals spread out across the species in each plot. We removed the pith, phloem, and bark, measured fresh volume by water displacement and determined dry mass after drying for 72 h at 70 °C (Cornwell *et al.* 2006). Meanwhile, we choose ten species of hardwood and corkwood respectively, ten individuals per these species were sampled nearby
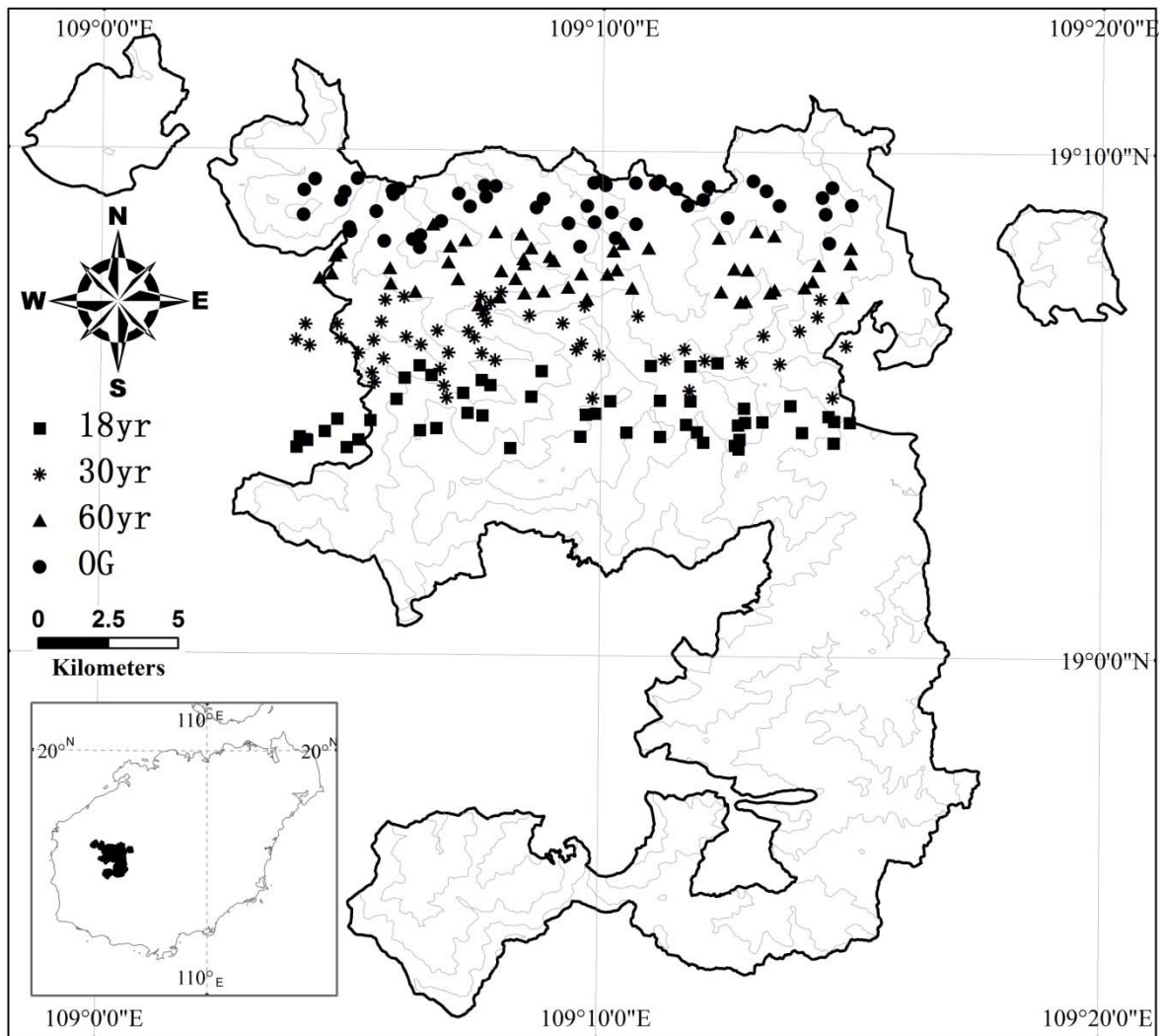
Fig. 1. A map with location of plots in Bawangling Forest Region on Hainan Island, south China (n=200). 18 yr, 18-year-fallow; 30 yr, 30-year-fallow; 60 yr, 60-year-fallow; OG, old growth forest.

the study sites, and cores of stem were taken with an increment borer (Haglof Increment Borer, Sweden) after sampling of branches. We found that the core density was linearly related to the branch density for hardwood ($\rho_{core} = 1.054\rho_{branch}$, $R^2 = 0.95$, $P < 0.0001$) and for corkwood ($\rho_{core} = 1.235\rho_{branch}$, $R^2 = 0.93$, $P < 0.0001$).

Species and functional diversity

We examined species diversity and functional diversity in each plot. In this paper, we characterize species diversity by species richness, i.e. the number of species in a quadrat. We characterize functional diversity, by functional richness (FRic), which is estimated by the convex hull volume, an n-dimensional measure of the volume of trait space

occupied by species in a community (Cornwell *et al.* 2006) and calculated it for all six traits together. We estimated by using the FD package in R with the function dbFD (Laliberté & Legendre 2010).

To assess how species diversity and functional diversity change during succession, analysis of variance (one-way ANOVA) were used and Tukey HSD multiple comparisons were conducted when there were significant differences ($P < 0.05$). To evaluate relationship between functional diversity and species diversity within each stage of succession, a regression model was used to examine the relationship between functional diversity and species diversity when all stages of succession were combined, we selected the best
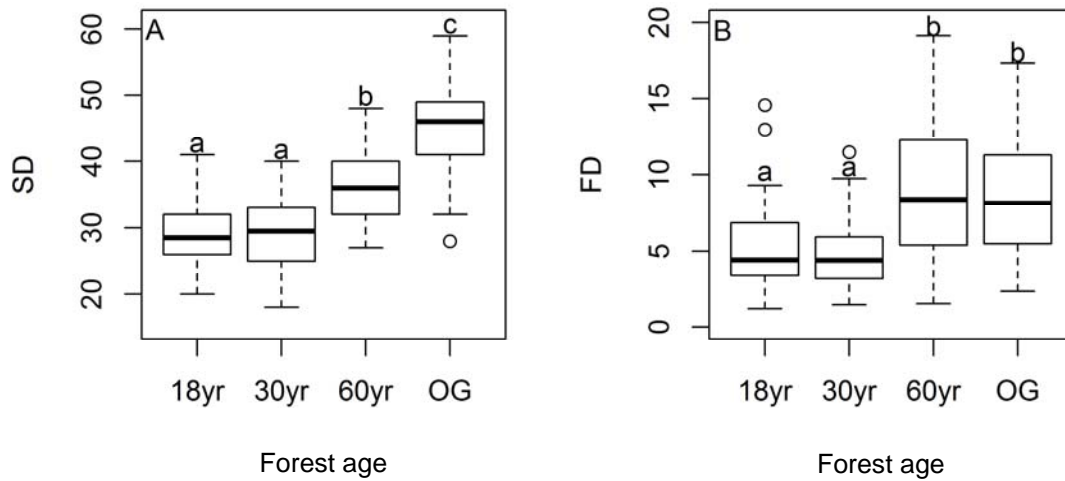
Fig. 2. Variations of species richness (SD) and functional richness (FD) along a successional gradient.

Table 1. Description of regression models for the relation between functional richness (FD) and species richness (SD). The logistic model has been selected for smallest Akaike Information Criterion (AIC)*.

Model	Equation	AIC	P
Logistic model	FD=12.344/(1+exp ((32.662-SD)/7.248))	927.1	<0.0001
Logarithmic model	FD=11.3403*lnSD-33.0382	1038.1	<0.0001
Linear model	FD=0.32*SD-4.25213	1040.2	<0.0001

*see Johnson & Omland (2004).

fitting model from linear model, logarithmic model and logistic model by the smallest Akaike's information criterion (AIC) (Johnson & Omland 2004). All statistical analyses were performed with R 2.14.1 Program (R Development Core Team 2011).

Results

Species and functional diversity change during succession

Species richness increased with the process of secondary succession (Fig. 2A), although difference was not significant between the first two stages (18- and 30-year-old fallows). Functional diversity also had the trend of increasing with the recovery year. Functional richness in the former two stages of succession was significantly lower than that in latter two stages (Fig. 2B). However, differences were not significant within the former two stages and the latter two stages.

Relationship between functional diversity and species diversity

Significant linear relations between functional diversity and species diversity existed within each stage of succession, indicating that functional diversity could be well predicted by species diversity (Fig. 3). Meanwhile, the slope of linear regression in 60-year-old fallow was higher than that in other three forest types. A sigmoid logistic relation between functional diversity and species diversity was found when all the stages of succession were combined (Fig. 4) after model selection (Table 1).

Discussion

Variation of species and functional diversity during succession

In accordance with our prediction, the species and functional diversity increased with succession (Fig. 2). Species diversity can be influenced by site age since abandonment in tropical forest succession (Chinea 2002; Mani & Parthasarathy 2009), which may be attributed to the increase of seed sources and habitat conditions such as a moisture gradient, etc. that improved gradually (Jiao *et al.* 2012; Teketay 2005).

Functional diversity significantly differed between the former two successional stages and the latter two successional stages. However, differences were not significant within the former two stages of succession and the latter two stages of succession. The pattern suggests that in the recovery periods of 18-30 years and 60 years-old growth, functional diversity changed slightly though some species recruited into the community with
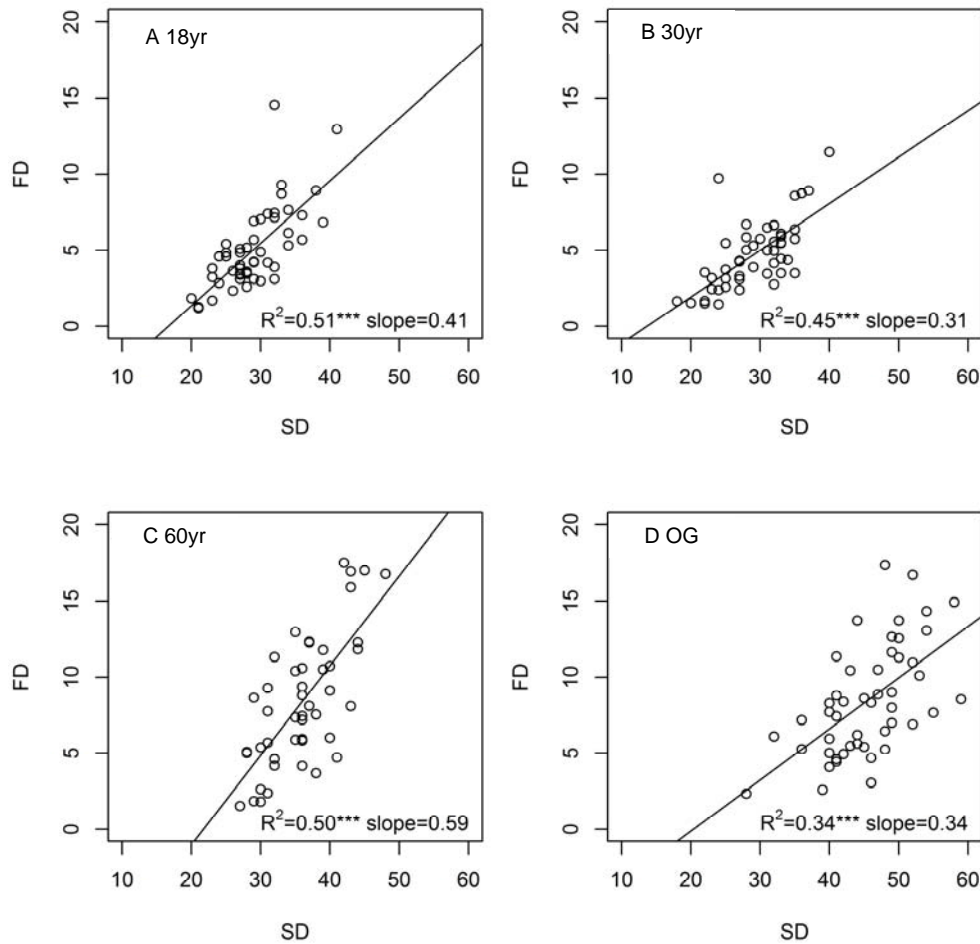
Fig. 3. Relationship between functional richness (FD) and species richness (SD) within each successional stage.

increasing recovery year. This pattern should result from newly recruited individuals functional by similar to the ones already present in the community (Lohbeck *et al.* 2011) and the fact that with a higher number of species already present in the community, the chance that 'new' species or functional types disperse to a site should decrease (Schmid *et al.* 2002). However, in recovery period from 30 years to 60 years, functional diversity increased significantly. This suggested that functional redundancy exists during the early and late stages of secondary succession (Laliberte *et al.* 2010; Paquette & Messier 2011).

Relationship between functional diversity and species diversity during succession

Functional diversity increases generally with species diversity (Bihn *et al.* 2010; Lohbeck *et al.* 2011), even though species diversity and functional diversity may also be uncoupled, as species diversity is hypothesized to be limited by the regional species pool, whereas functional diversity is hypothesized to be limited by the local availability of niches (Schmid *et al.* 2002).

A positive linear relationship of FD-SD within each successional stage (Fig. 3) indicates that each species has relatively unique sets of traits (Flynn *et al.* 2009) and functional complementarity always appears in some respects among different species.

Overall, a sigmoid curve can describe the relationship between functional diversity and species diversity in the secondary succession: low increase rate is found in early and late successional stages and high increase rate is predicted in middle successional stage (Fig. 4). The sigmoid logistic pattern of FD-SD suggests that two-phase functional redundancy is present during this secondary forest succession. Because the resilience of ecosystem is tightly related to the maintenance or recovery of ecosystem functioning under changing environmental conditions or disturbance events (Walker *et al.* 1999) and functional redundancy, the core of theory relates changes in ecosystem
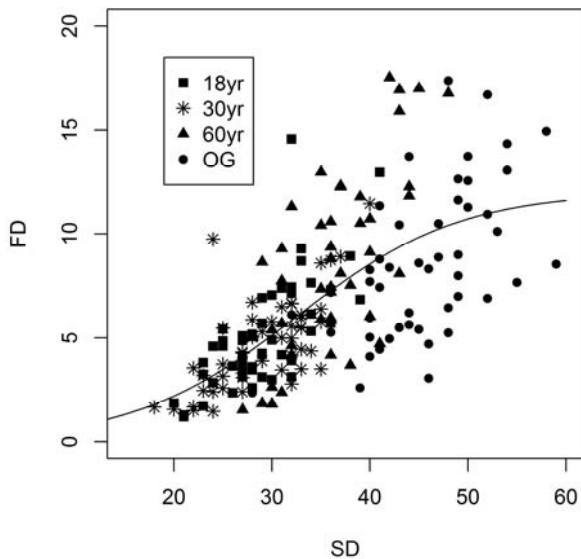
Fig. 4. A sigmoid logistic relation between functional richness (FD) and species richness (SD) when all successional stages were combined. The symbols are the same as in Fig.1.

functioning to species loss (Micheli & Halpern 2005) rather than functional diversity improving ecological resilience of ecosystem (Flynn *et al.* 2009; Laliberte *et al.* 2010); the forest of middle stage of succession becomes sensitive to disturbance regimes or change of environmental conditions caused by human activities.

In early successional stage, unfavourable conditions such as low canopy density and high light intensity would make only some pioneer species to survive in it. These species may have similar trait value owing to habitat filtering (Cornwell *et al.* 2006; Katabuchi *et al.* 2011). Thus high functional redundancy is expected to exist in this stage.

With the progress of succession, some shade-tolerant species, which are species not yet present in the plot, with functional strategies complementary to the ones already present (Lohbeck *et al.* 2011) recruit into the community, the coexistence of different functional groups make functional diversity increase gradually. Because traits determine how an organism extracts resources from its environment (McGill *et al.* 2006), as FD increases, a community increases its partitioning of the total available resources (Cadotte *et al.* 2011). The rapid increase of functional richness also indicates that the key period of species competition takes place and low functional redundancy is expected during the middle stage of succession (30 - 60 years), which is

mainly caused by niche differentiation (Hishi 2007; Kraft *et al.* 2008).

Finally, for low light availability, shade-tolerant species dominate in community at the later stage of succession and functional diversity may remain constant although some rare species may also be added to the community. Meanwhile, enough high species richness results in some species having similar trait value. Consequently, high functional redundancy is predicted in this stage (Laliberté & Legendre 2010; Paquette & Messier 2011).

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