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Spatiotemporal Patterns and Dynamics of Species Richness and Abundance of Woody Plant Functional Groups in a Tropical Forest Landscape of Hainan Island, South China

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Abstract

Tropical forests are among the most species-diverse ecosystems on Earth. Their structures and ecological functions are complex to understand. Functional group is defined as a group of species that play similar roles in an ecosystem. The functional group approach has been regarded as an effective way of linking the compositions of complex ecosystems with their ecological functions. To understand the variation of functional groups in species-rich ecosystems after disturbance, the present study investigated the spatial pattern and temporal dynamics of woody plants in a typically fragmented natural forest landscape of Hainan Island in South China. The study area was classified into eight landscape types based on vegetation type, disturbance manner and the time of recovery. The woody plant species were aggregated into seven functional groups based on the growth form, successional status and plant size. The results gained from the present study showed that all functional groups, except for the emergent and canopy tree species, were present in all eight landscape types. Each landscape type had different numbers of dominant functional groups. There are similar species richness and stem abundance structure among functional groups between mid-successional clear cut lowland rainforest and old growth tropical coniferous forest. This similarity exists in selective logged lowland rainforest and old-growth lowland rainforest, as well as among landscape types of montane rainforest. The functional groups with the same successional status had similar patterns of species richness and stem abundance ratios among different landscape types. The variation patterns of functional groups along the successional stages in terms of species richness and stem abundance among the tropical lowland rainforest landscape types were more similar to each other than those in the tropical montane rainforest landscape types. This study provides further support for the competition-colonization tradeoff and successional niche theory as opposed to models of neutrality and ecological equivalence.

Key words: forest landscape types; functional groups; Hainan Island; recovery dynamics; spatial variation; species diversity; stem abundance; tropical forests.

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Among the ecosystems with the richest biodiversity on Earth (Wilson 1995), tropical forests are increasingly affected by various disturbances. A central challenge for humankind is to protect, restore and manage these forest resources effectively and sustainably. Although disturbance may enhance species diversity by reducing the competitive exclusion caused by dominant species (Connell 1978), intensive and repeated human disturbance can cause destruction of integrative landscape patterns and ecosystem processes. Landscape fragmentation can increase the degree of isolation among forest remnants and reduce the size and quality of habitats, and

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may therefore affect the distribution patterns and population structure of species. Extensive fragmentation may also lead to local extinction of some sensitive species (Wilson 1995; Turner and Gardner 2001). In order to restore the ecosystems effectively, understanding the nature and dynamics of the disturbed forest landscapes is needed. An important way is to assess the spatiotemporal patterns and dynamics of species in the fragmented landscapes, and analyze not only the effect of biodiversity change on landscape structure but also the response of biodiversity to landscape changes over time (Foster 2002).

Because of their great species richness and high complexity of community structure, tropical forests are more complex to understand, when compared with other ecosystems. Application of the theory of functional groups in research may be one of the best ways to solve this problem. Although there are diverse and controversial viewpoints on the concepts and classifications of functional groups (Denslow 1996; Lavorel et al. 1997; Peter et al. 2000), consensus that a functional group is a species assemblage with similar responses or effect-functional traits in an ecosystem is emerging (Denslow 1996). Classifying species into functional groups may help explicitly understand the relationships among environmental factors and the patterns and processes of ecosystems (Vitousek and Hooper 1993). This concept (functional group or plant functional type) has been applied in a wide range of spatial scales, from a plant community, to an ecosystem and from a watershed to a large region.

Types and amounts of functional groups may differ in species pool of certain biomes because the classification of functional groups usually depends on the scale and objectives in question (Denslow 1996; Skarpe 1996). Therefore, a vital issue is how to choose functional traits on the basis of certain scale for the classifications of functional groups (Duckworth et al. 2000). At a community or an ecosystem level, comparative detailed plant traits for the classification usually involve the morphological, structural, physiological and life-history characteristics (Denslow 1996; French and Picozzi 2002; Grubb 2002; Mason et al. 2005). At a landscape or a regional scale, relatively coarse classifications are chosen in order to predict the broad distribution of vegetation and their dynamics (Prentice and Webb III 1998; Paruelo et al. 2001). In the present study we revised an existing classification of functional groups on the basis of wood density (Peter et al. 2000) in order to meet our research objectives in tropical forests on Hainan Island.

Today, in landscape ecology of tropical forests, studying the relationships between functional groups and forest fragments has become a major focus (Metzger 2000; Hill and Curran 2003; Pausas 2003). But few studies have discussed spatial patterns and temporal dynamics of the functional groups simultaneously at the landscape scale. In the present study, we conducted an intensive field survey with 135 sampling plots across eight natural forest landscape types in the Bawangling tropical forest region of Hainan Island. Our objectives were to address the following questions (i) How can we classify forest landscape types and functional groups adapting for analysis of tropical woody plant species at the landscape scale? (ii) Are there any variation trends of functional groups concerning species richness and stem abundance among different forest landscape types? (iii) Are there significant changes in species richness and stem abundance for functional groups at the different successional stages?

Results

Composition of taxa in each functional group

There was no equal frequency distribution in the number of families (nonparametric χ^2 test, $\chi^2 = 54.817$, degrees of freedom d.f. $= 6$, $P < 0.001$), genus ($\chi^2 = 176.699$, d.f. $= 6$, $P < 0.001$) and species ($\chi^2 = 470.462$, d.f. $= 6$, $P < 0.001$) among seven functional groups. F6 was the largest, including 60 families, 130 genera, and 267 species, representing 25.2%, 31.0% and 35.6% of the totals, respectively. F7 was next largest, which included 54 families, 95 genera, and 152 species, representing 22.7%, 22.6% and 20.3% of the totals, respectively. F1 and F4 had the lowest numbers of taxa. F1 included 17 families, 19 genera and 24 species, or 7.1%, 4.5%, and 3.2% of the respective totals, and F4 included 16 families, 20 genera, and 25 species, or 6.7%, 4.8% and 3.3% of the respective totals (Figure 1).

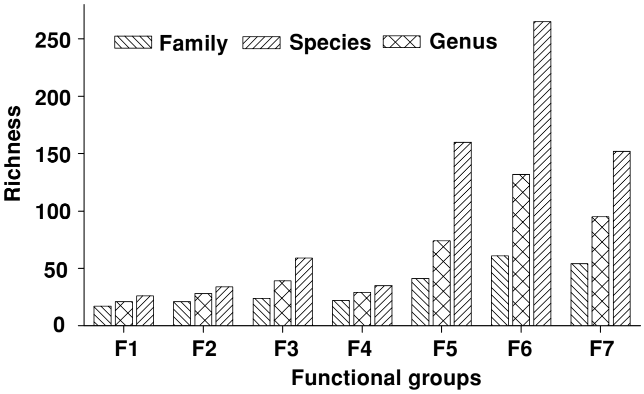

Figure 1. Composition of family, genus and species in each functional group.

F1, early-successional shrub species; F2, mid-successional shrub species; F3, late-successional shrub species; F4, early-successional tree species; F5, mid-successional tree species; F6, late-successional tree species; F7, emergent and canopy tree species.

Variation of functional groups in different landscape types

Changes of species richness within landscape types

We compared species richness among the functional groups for each landscape type using the non-parameter Kruskal-Wallis test (Table 1). Significant differences were found in LT5, LT6, LT7 and LT8. There were no consistent significant differences among the landscape types of lowland rainforest. Differences in LT4 were similar to that among landscape types of montane rainforest and LT8. No significant difference in species richness among the functional groups was found for LT2. Little difference for other landscape types of lowland rainforest was observed.

Distribution of species richness (mean ± *SE*) among seven functional groups was tested for each forest landscape type by multi-test (Figure 2). F6 was richest, comprising 48.08% of all species in LT6 and 44.26% of all species in LT7, and the richness was significantly higher than those of other functional groups ($P < 0.05$). The species richness of F5 and F6 was relatively high in LT3, LT4, LT5 and LT8. A significant difference could be found among these and other functional groups ($P < 0.05$), except for F6 and F2 in LT3. Although the species richness of F2, F3, F5, F6 in LT1 was comparatively great, we found no significant differences between these functional groups. The species richness of F5 in LT2 attained 35.45% of the total species number, and there were significant differences between it and other functional groups ($P < 0.05$), except for F3. On the other hand, there was comparatively lower species richness in some functional groups. The species richness of F1, F4 and F7 in LT1 were low, and we found significant differences between F1 and other functional groups ($P < 0.05$), but no significant difference between F4, F7 and other functional groups. Relatively low species richness occurred in F1, F2, F3, F4, F6 and F7 in LT2 and LT3, and there was significant difference between F2 and F3 ($P < 0.05$) in LT3. The species richness of F1, F2, F4 and F7 in LT4 were comparably low, and a significant difference was found between them and other functional groups ($P < 0.05$). F1 and F4 in LT5, LT6 and LT7 showed the lowest number of species, and there were significant differences among F1, F4 and other functional groups in LT6 ($P < 0.05$). The species richness of F7 and F4 in LT8 were low, and a significant difference could be found between F7 and other functional groups, but no significant differences between F4 and F1, F2 and F3.

Furthermore, F1 and F4 showed relatively high species richness in LT2 and LT8.The species richness of F3 and F6 was greater in LT1, LT4 of lowland rainforest and all landscape types of montane rainforest. The species richness of F7 was relatively high in LT4 of lowland rainforest and all landscape types of montane rainforest.

Change of stem abundance of functional groups in different landscape types

We compared stem abundance among seven functional groups for each landscape type (Table 1), whereby significant difference was found among all functional groups and in all eight landscape types.

We also tested the distribution of the stem abundance of seven functional groups for each landscape type (Figure 3). Compared with other functional groups, F3 and F6 showed a higher abundance in every landscape type, and the significance was statistically significant ($P < 0.05$), except for the comparison between F3 and F5 in LT7. The stem abundance of F3, F5 and F6 were high in LT1, LT4 and LT8, and there were significant differences ($P < 0.05$) between them and other functional groups in the three landscape types, but no significant differences between F1, F2 and F3, and between F6 and F1 in LT8. The stem abundances of F3 and F5 were high in LT2, and there were significant differences ($P < 0.05$) between them and other functional groups. Values of the stem abundance of F1 to F6 were comparatively even in LT3, ranging from 10.30% to 26.01% of the total stems. Some functional groups had lower stem abundances in some landscape types. The stem abundance of F7 was lowest in LT1, LT2, LT3 and LT8, there were significant differences ($P < 0.05$) between it and other functional groups, but no significant difference between F7 and F4 in LT3. The stem abundance of F1, F4 and F7 were lower in LT4 and LT5, and there were significant differences

Table 1. The difference of species richness and stem abundance among functional groups in each forest landscape type

Indices	Forest landscape type							
	LT1	LT2	LT3	LT4	LT5	LT6	LT7	LT8
Richness	13.12*	8.54	18.00**	115.90***	100.71***	67.53***	161.98***	67.53***
Abundance	12.14**	4.63***	11.80*	83.97***	91.22***	63.45***	149.40***	63.45***

Data are the χ^2 values of non-parameter Kruskal-Wallis tests. LT1, early-successional stage; LT2, clear cutting at the early-successional stage; LT3, clear cutting at the mid-successional stage; LT4, old-growth landscape type in tropical lowland rainforests; LT5, landscape types with selective logging at the early-successional stage; LT6, with selective logging at mid-successional stage; LT7, old-growth landscape type in tropical montane rainforest; LT8, old-growth tropical coniferous forest landscape type. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

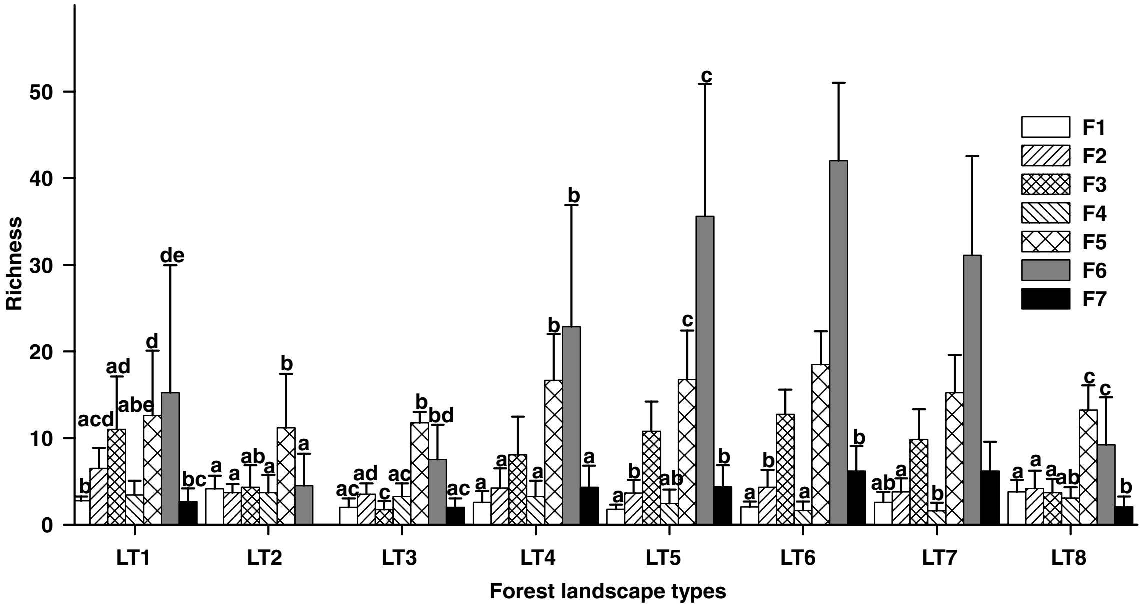

Figure 2. Distribution of species richness (mean ± *SD*) and multi-test among functional groups in each forest landscape type.

Different letters at the tops of columns show significant differences ($P < 0.05$) between functional groups in each forest landscape. F1, early-successional shrub species; F2, mid-successional shrub species; F3, late-successional shrub species; F4, early-successional tree species; F5, mid-successional tree species; F6, late-successional tree species; F7, emergent and canopy tree species; LT1, early-successional stage; LT2, clear cutting at the early-successional stage; LT3, clear cutting at the mid-successional stage; LT4, old-growth landscape type in tropical lowland rainforests; LT5, landscape types with selective logging at the early-successional stage; LT6, with selective logging at mid-successional stage; LT7, old-growth landscape type in tropical montane rainforest; LT8, old-growth tropical coniferous forest landscape type.

($P < 0.05$) between them and other functional groups, but no significant differences between F1, F4 and F2 in LT4. The stem abundances of F4 and F7 were lower in L6, and there were significant differences ($P < 0.05$) between them and other functional groups. The stem abundance of F4 was lowest in LT7, and there were significant differences ($P < 0.05$) between it and other functional groups.

Furthermore, the stem abundances of F1 and F4 were high in LT1, LT2 and LT8. F4 showed a relatively even stem abundance in LT2, LT3 and LT4 of the lowland rainforest. The stem abundance of F2 was relatively high in landscape types of the lowland rainforest and LT8, with an average value of 45.50. The stem abundance of F5 was highest (with an average value of 155.88) in LT1, LT2 and LT4 of the lowland rainforest. This functional group showed also relatively high stem abundance (82.77) in landscape types of montane rainforest and LT8. The stem abundances of F3 and F6 were relatively high in LT1 and LT4 of the lowland rainforest and landscape types of montane rainforest, with the means of 158.37 and 161.61, respectively. Similarly, higher stem abundance (201.33±139.58) was found in F3 of LT2. The stem abundance of F7 was relatively high in LT4 of lowland rainforest and LT6, LT7 of montane rainforest.

Dynamics of functional groups in community succession

Changes of species richness over time

In the lowland rainforest, when considering the recovery series, significant difference ($P < 0.01$) in species richness was only found between F3 and F6 (Table 2; Figure 4). F1 and F4 showed a relatively high species richness in landscape types at the early-successional stage, with an initial increase followed by a gradual decrease over successional time. However, the species richness of F1 at the mid-successional stage was lowest. A similar temporal development of species richness was observed in F2 and F4 (i.e. LT1 > LT4 > LT2 > LT3). There were similar trends of species richness for F5, F6 and F7 (i.e. LT4 > LT1 > LT3 > LT2) (Figure 4).

In the montane rainforest, significant difference in species richness was found between F3 ($P < 0.01$) and F6 ($P < 0.001$). No or marginal significant difference was observed between other groups and different landscape types (Table 2; Figure 4). The species richness of F1 and F7 increased gradually with the recovery time. The species richness of F2 was lowest in the landscape types at the early-successional stage, and then attained the peak of curves in landscape types at the mid-successional stage, and at last decreased again at the old-aged

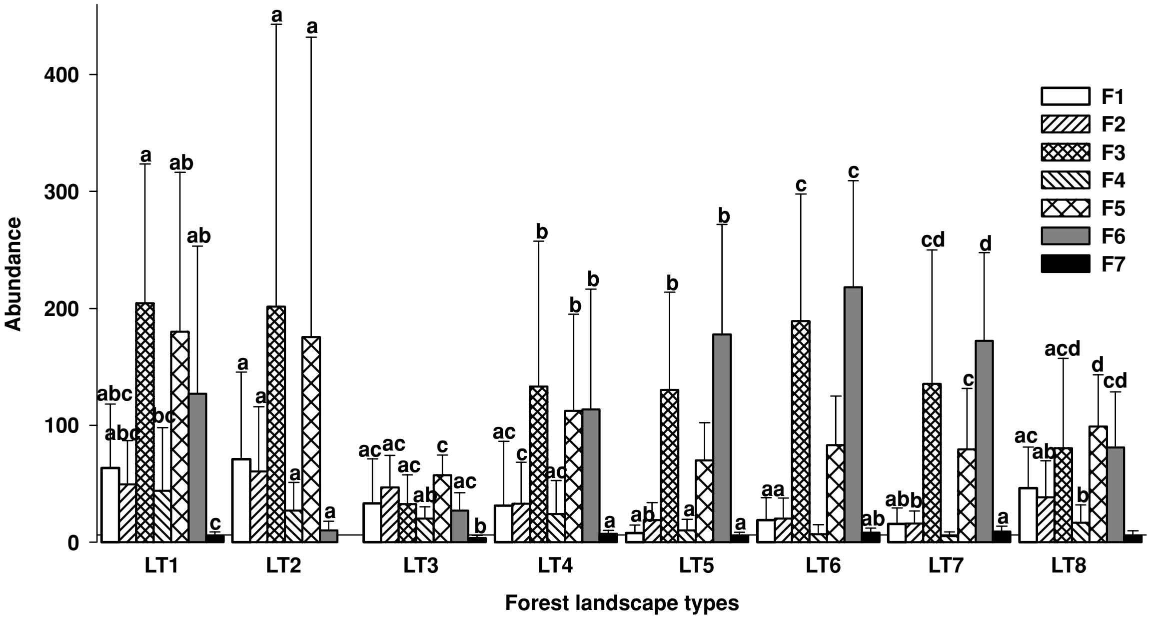

Figure 3. Distribution of abundance (mean ± *SD*) and multi-test among functional groups in each forest landscape type.

Different letters at the tops of columns show significant differences ($P < 0.05$) between functional groups in each forest landscape type. F1, early-successional shrub species; F2, mid-successional shrub species; F3, late-successional shrub species; F4, early-successional tree species; F5, mid-successional tree species; F6, late-successional tree species; F7, emergent and canopy tree species; LT1, early-successional stage; LT2, clear cutting at the early-successional stage; LT3, clear cutting at the mid-successional stage; LT4, old-growth landscape type in tropical lowland rainforests; LT5, landscape types with selective logging at the early-successional stage; LT6, with selective logging at mid-successional stage; LT7, old-growth landscape type in tropical montane rainforest; LT8, old-growth tropical coniferous forest landscape type.

landscape types. The variational curves of F3, F6 and F5 were similar to F2, but the lowest value of species richness was in the old-growth landscape types rather than the lowest value of F2 at the early-successional stage. Unlike other functional groups, the species richness of F4 decreased gradually from the early-successional landscape type to the old-aged landscape type.

Changes of stem abundance over time

In the lowland rainforest, significant differences ($P < 0.01$) in stem abundance were found between F3 and F6, but no or marginal significant differences of other functional groups were found between the different landscape types (Table 2; Figure 4). The shrub functional groups (F1, F2, F3), F4 and F5 presented the highest stem abundances in the early-successional landscape types, such as F3, F4 and F5 in LT1, and F1 and F2 in LT2. The stem abundances of these functional groups decreased gradually at the later successional stages. The change trend of the stem abundance of F6 was different than those of other functional groups: it was highest in LT1 and appeared lowest in LT2 and turned out to be increasing in LT3 and attained the same level with LT1 in the undisturbed landscape type LT4. Due to the serious logging disturbance, F7 was not found in LT2. Its stem abundance increased gradually from LT3 to LT1 and the undisturbed landscape type LT4.

In the montane rainforest, there was a significant difference in stem abundance between F6 ($P < 0.01$) and F7 ($P < 0.001$), but no significant difference was found in other functional groups between the different landscape types (Table 2). The stem abundance of F1 and F4 decreased gradually over succession (Figure 4). F2 and F6 showed a similar trend of stem abundance: it peaked in LT6, and dropped to the lowest value in the undisturbed landscape type LT7 (Figure 4). Similarly, F3 and F5 reached the greatest value in the landscape type at the mid-successional stage and showed the lowest value in the landscape type at the early-successional stage (Figure 4). The stem abundance of F7 increased with increasing succession.

Discussion

Determination of the successional status of species in the functional classification

There is a long history of classifying species into functional groups by the view of community succession. In the 1960s and 1970s, Budowski (1965) and Whittaker (1975) divided

Table 2. The difference of species richness and stem abundance of each functional group in different recovery series

Vegetation type	Indices	Functional group						
		F1	F2	F3	F4	F5	F6	F7
Lowland rainforest	Richness	6.53	4.21	10.88**	0.41	6.98*	11.03**	3.42
	Abundance	5.02	3.25	5.07**	1.31	3.34*	10.30**	3.59
Montane rainforest	Richness	6.52	1.97	8.65**	5.77	7.22*	11.80***	4.6
	Abundance	6.91*	0.29	5.00*	2.31	0.51	3.30**	10.40***

Data are the χ^2 values of non-parameter Kruskal-Wallis tests. F1, early-successional shrub species; F2, mid-successional shrub species; F3, late-successional shrub species; F4, early-successional tree species; F5, mid-successional tree species; F6, late-successional tree species; F7, emergent and canopy tree species. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

plant species into an early-successional group and a late-successional group (Shugart 1997). Since then, the classification has become more and more explicitly represented in the application of multi-traits, such as tolerance to light, habit, growth strategy and so on. For example, to group early-successional species and late-successional species, Bazzaz (1979) chose the traits of light adaptation and carbon fixation, while Whitmore (1989) set up classification on the basis of seedling regeneration in gap, building, mature and degenerate phases. However, Whitmore also pointed out coarseness of the two-group method and suggested to subdivide species into more groups. A recent development was made to combine the succession theory with more functional traits (e.g. wood density, seed size, potential maximum heights, and etc.) when setting up a functional classification (Condit et al. 1996; Kammesheidt 2000; Peter et al. 2000; Verburg and van Eijk-Bos 2003). As mentioned above, determining the successional status of species plays an important role in forming functional classification in relation to recovery ecology. However, there are many difficulties to classify species into functional groups when most biological traits of species remain unknown in ecosystems, especially in tropical forests. The establishment of an applicable classification usually depends on data availability of the biological traits. Fortunately the related-successional traits of most species, such as wood density and seed size are often recorded in forestry databases and Floras.

Fast-growing trees with low wood density often occur in disturbed environments, in contrast to slow-growing trees with higher wood density in undisturbed habitats (Thomas 1996; Suzuki 1999). Thus, this trait has been used as a useful indicator for determining successional status of species (Swaine and Whitmore 1988; Peter et al. 2000; Ter Steege and Hammond 2001). Sizes and masses of seeds are negatively correlated with the seed dispersal capability (Westoby et al. 2002) and seed dormancy (Dalling and Hubbell 2002), but are positively correlated with shade-tolerance (Coomes and Grubb 2003). Thereby, these traits have been also regarded as important factors to discriminate between early and late successional species (Swaine and Whitmore 1988). In the present study, we tested the correlation between the seed size and wood density (Figure 5) and the results showed a positive relation between the two parameters ($R = 0.545$, $P < 0.001$). Because it is normally easier to obtain data on seed size from published reports than to obtain data on seed mass, the seed sizes were used in this study for determining the successional status.

Variation of functional groups along with spatiotemporal changes

The pattern and dynamics of functional groups in space and time are closely correlated with their resource use strategies. The early-successional tree or shrub groups usually include those photophilic, fast-growing species with large quantities of well-dispersed seeds. Consequently, they tolerate severely disturbed sites after selective logging and clear logging in LT1 and LT2, where the recovering period was shorter (Figures 2–4). Similar composition of early-successional groups appeared in LT8, an undisturbed tropical coniferous forest, where species richness and stem abundance of F1 and F4 were higher than those of the other undisturbed landscape types (LT4 and LT7). This similarity may have been caused by the characteristics of the coniferous forests, such as the relatively discontinuous canopy, more incidental light at the ground level, high understory temperature, and dry soil conditions. Those traits owned by species in F1 and F4, such as large quantities of well-dispersed seeds and light demanding, may lead them to establish successfully prior to those species in mid and late successional groups in LT1, LT2 and LT8, at the same time their fast-growth ability in a resourceful site ensured that they are dominant in richness and abundance within early successional landscape types (Rees et al. 2001). Similar to the results in the present study, Verburg and van Eijk-Bos (2003) found a high fraction of softwood stems during the primary years of succession. With the successional development, the fraction of softwood stems gradually decreased. Verburg and van Eijk-Bos (2003) noticed that high fractions of softwood stems occurred in the early successional stage, and that they tended to decrease along with stand development. Similar results were also found in our study. Collectively, these results further support two mechanisms of competition-colonization tradeoff and successional

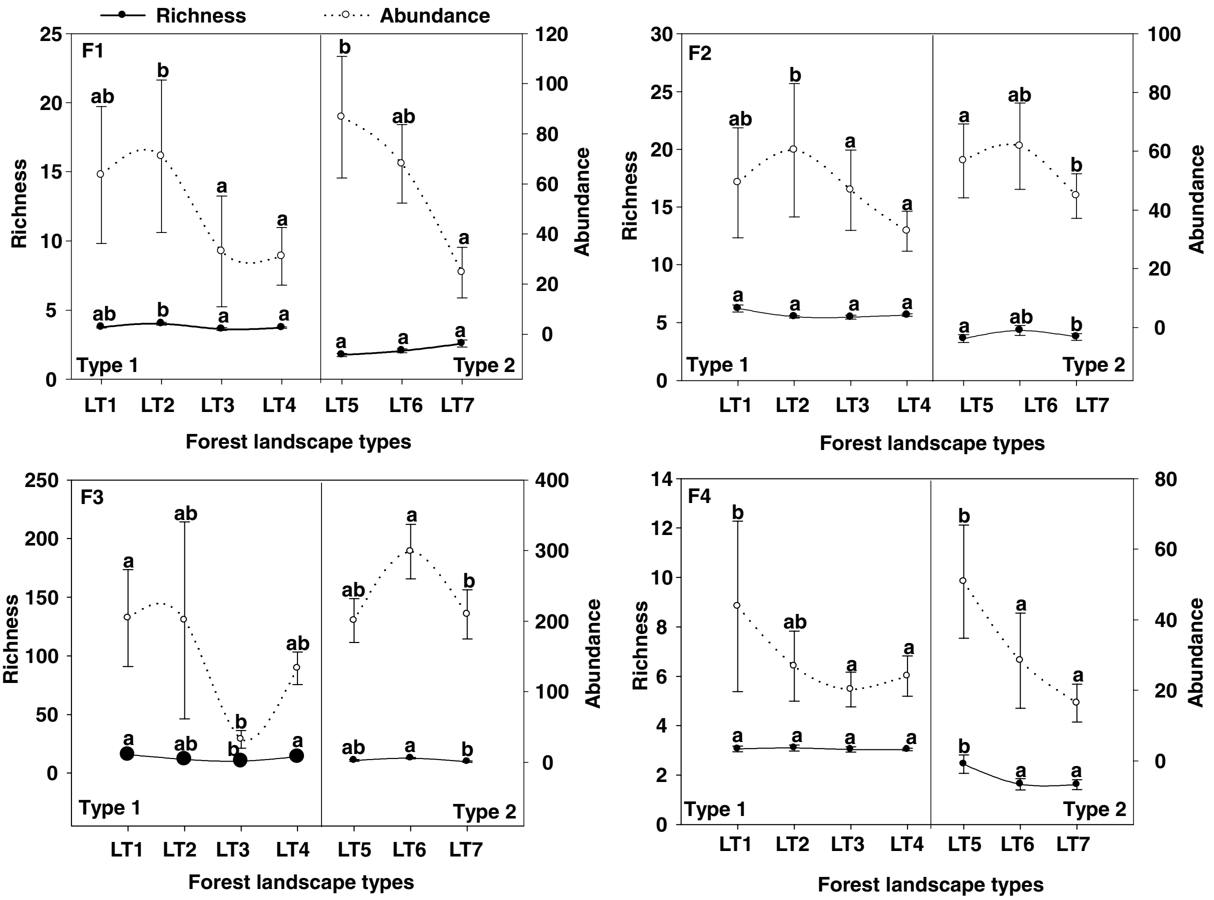

Figure 4. Distribution of species richness (mean ± *SD*) and abundance (mean ± *SD*) of each functional group in different recovery series.

Type 1, lowland rainforest; type 2, montane rainforest. The same letter on the figures between functional groups shows no significant difference along recovery time. LT1, early-successional stage; LT2, clear cutting at the early-successional stage; LT3, clear cutting at the mid-successional stage; LT4, old-growth landscape type in tropical lowland rainforests; LT5, landscape types with selective logging at the early-successional stage; LT6, with selective logging at mid-successional stage; LT7, old-growth landscape type in tropical montane rainforest; LT8, old-growth tropical coniferous forest landscape type.

niche (Stephen and Mark 1998). As mid-successional groups, F2 and F5, although sometimes conforming to some characteristics of early successional species, have some special features, for example, more diverse canopy and leaf characteristics (Kammesheidt 2000), bigger seeds, older age at first reproduction, longer life-span and greater height at maturity than did early-successional species (Chapin III et al. 1994). Those traits may explain why their sensibility to successional development was lower than the early-successional groups on variation of species richness and stem abundance among forest landscape types. F3 and F6, the two late-successional groups, have some characteristics different from others, including a relatively lower fecundity, a shorter dispersal ability, a slower growth, a longer longevity, a later maturation, the longer-lived leaves and a high specific leaf area (Rees et al. 2001). The characteristics of late-successional groups may determine their dominance among functional groups in most forest landscape types (Figures 2 and 3). Some characteristics, including the ability to regenerate, grow and survive under closed canopy conditions and the competitiveness under resource-poor conditions (Montagnini and Jordan 2005), gave a guarantee of relatively high fraction of late-successional groups in LT1, LT2 and LT3.

The interaction among functional groups is also an important factor for determining the spatial pattern of functional groups in different landscape types. There are relatively more similar proportions concerning species richness and stem abundance among functional groups in more-disturbed, short-recovered landscape types (e.g. LT3) than in less-disturbed (or non-disturbed), long-recovered landscape types (e.g. LT7). This may be because in severe environments, facilitation plays a major role that is responsible for even distribution of functional groups, while inhibition affects uneven distribution of functional groups in

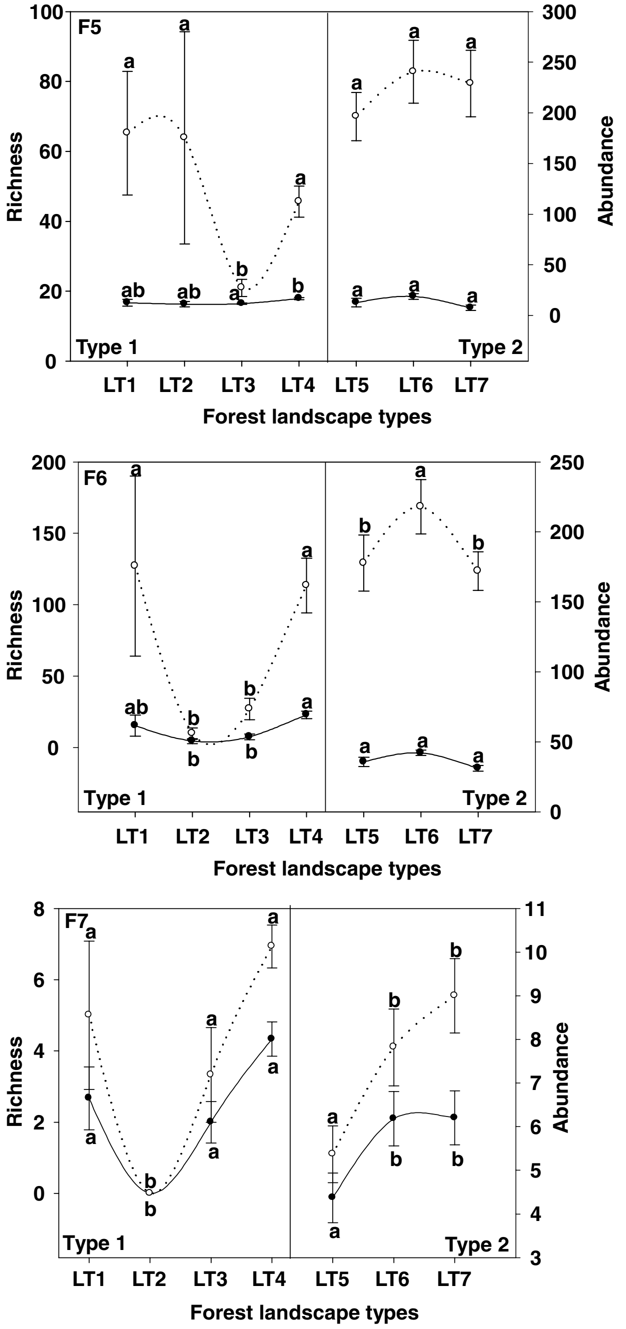

Figure 4. Continued.

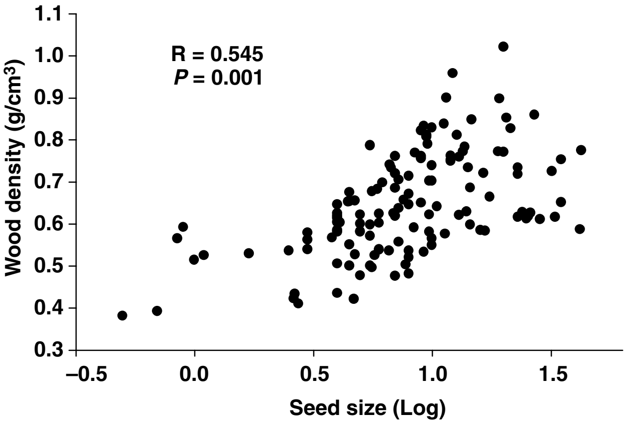

Figure 5. The relationship between species-specific seed size and wood density.

more favorable environments. In more-disturbed, short-restored landscape types, the fast-growing species in F1 and F4 can not only improve the environment, for example, increasing soil humidity, decreasing ground temperature, augment the availability of resources for mid- and late-successional functional groups, but can also provide habitat for seed-dispersing animals (Denslow 1996). This may, to a certain extent, improve the colonizing opportunity for mid- and late-successional functional groups in severely-disturbed environments, and may result in compromise concerning species richness and stem abundance between functional groups with less species or individuals of species and functional groups with more but immigrating less in more-disturbed, short-restored landscape types. Otherwise, the distribution pattern of functional groups in disturbed-landscape types (e.g. LT6) may also confirm the hypothesis that if sites have not been heavily disturbed, microhabitat may be more favorable for all species, and functional groups dominated only depend simply on which species belongs to the special functional group that arrived first (Montagnini and Jordan 2005). In LT4 and LT7, the old-growth forest landscape types, the dominance of late-successional functional groups, especially F6 and the increase of canopy and emergent functional group F7 (Figures 2 and 3) indicated that they, to a large extent, reduced the colonization niche breadth of early- and partly mid-successional functional groups. However, Rees et al. (2001) stated that in undisturbed landscapes, late-successional functional groups eventually exclude early-successional functional groups competitively, mainly because they reduce resources beneath the levels required by the early-successional groups. As gamblers (Montagnini and Jordan 2005), species of early-successional and partial mid-successional groups increase the likelihood arriving in gap just based on reproductive strategy.

Disturbance is the dominant mechanism causing spatial heterogeneity (Chaneton and Facelli 1991). It is also the prerequisite to succession for community and can further affect the distribution of functional groups. The variable trends of species richness and stem abundance within a functional group in different forest landscape types demonstrate that shrub successional groups are more tolerant to disturbance than tree successional groups, and that the distribution pattern of emergent and canopy trees (F7) is also closely correlative with disturbance types, intensity and recovery time. The species richness and stem abundance of F7 tend to increase, from clear-cutting, selective cutting to undisturbed forests and from early-successional, mid-successional to old-growth forests. The disappearance of F7 in LT2 may have been caused by the high-intensity disturbance (clear logging).

Climate, soil, topography and bio-geographical history are also predominant determinants of distribution patterns of functional groups in different temporal-spatial scales (Denslow 1996). In the present study, the among-site variation in species richness and stem abundance of functional groups in each forest landscape type (Figures 2 and 3) may be the consequence of interaction between topographical factors and soil properties. The mid-successional functional groups F2 and F5 may have better adapted to fluctuating temperatures, which contributes to their wide distribution along with altitude gradients (Zhang ZD and Zang RG, unpubl. data, 2006). The increase of early-successional functional groups F1 and F4 was along gradients from fertile to arid sites. However, it is not clear how the distribution of functional groups relates to the environment gradients.

Materials and Methods

Study site

The study site is located in the Bawangling forest region (18°50′−9°05′N, 109°05′−109°25′E), an area of 49 500 ha between Changjiang County and Baisha County, Hainan Province, China. The elevation of the area is between approximately 100 m and 1655 m, and the area is characterized by a tropical monsoon climate with a distinct wet season from May to October and a dry season from November to April. The annual precipitation is 1 500–2 000 mm and the mean annual temperature is 23.6 °C. Soils in the area are among latosols and are developed from granite.

In this forest region, five vegetation types exist including tropical lowland rainforest, tropical montane rainforest, montane evergreen forest, montane evergreen dwarf forest and tropical coniferous forest. Prior to 1957, most parts of the Bawangling forest region were covered by these types of old growth tropical forests. Deforestation occurred due mainly to natural disturbances (such as fire, monsoon wind, and insect, etc.) and the traditional shifting cultivation by the local people. In the 1960s commercial timber logging became the main cause of deforestation (Chen and Yang 2001). During the 1980s, because of decreased tropical forests, timber harvest changed from clear cutting to high intensity of selective logging and low intensity of selective logging. Since 1994 harvest has been banned to protect and restore the degraded forests. Because of the severe and repeated anthropogenic disturbance in the past forty years, forest landscapes in Bawangling became increasingly fragmented.

Data collection

A total of 135 sample plots (20 m × 20 m) were laid systematically across the forest region on a 1 × 1 km or 2 × 1 km grid. At each crossed point (node) of four neighboring 1 × 1 km grid cells we chose a plot for vegetation investigation. These sample plots covered a total area of 5.95 ha occurring in eight landscape types (Table 3). Within each sample plot all stems of diameter at breast height (DBH) ≥1cm were counted, measured and identified to the species level. We also recorded the height and canopy size of free-standing woody plants (DBH ≥1cm). Determination of the time since the last disturbance and of the disturbance type in each sample plot was made based on timber-logging archives of the Forestry Bureau of Bawangling. In addition, experienced loggers were interviewed for detailed information on harvesting operation.

Classification of landscape types and aggregation of functional groups

We investigated three vegetation types in Bawangling: (i) tropical lowland rainforest; (ii) tropical montane rainforest; and (iii) tropical coniferous forest. In these vegetation types, forest landscape types involved the fragments of old-growth forests and secondary forests developed at various stages. We classified these fragments into eight landscape types (LT1–LT8) based on vegetation type, disturbance type and the recovering time since the last disturbance. The eight landscape types include landscape types with selective logging at the early-successional stage (LT1), with clear cutting at the early-successional stage (LT2), clear cutting at the mid-successional stage (LT3) and the old-growth landscape type (LT4) in tropical lowland rainforests, landscape types with selective logging at the early-successional stage (LT5), with selective logging at mid-successional stage (LT6) and the old-growth landscape type (LT7) in tropical montane rainforest and old-growth tropical coniferous forest landscape type (LT8). For more details see Table 3.

Although principles used for species aggregation into functional groups have been discussed widely (Box 1996; Gitay and Noble 1997; Lavorel et al. 1997), there is no universal classification rule for the development of functional groups. The type of classification depends mainly on the objective of the actual studies. Species similar in growth form, successional status or canopy structure are likely to have similar patterns of resource use, responses to disturbance patterns, and the rate and direction of succession following both natural and anthropogenic disturbances etc., respectively (Denslow 1996). In the present study we compiled available data on woody plant species composition from our field survey and the references (Chun 1964, 1965; Joint Working Group on Hainan Timber Research 1966; State Forestry Administration 2001). Woody species within each landscape type were classified using three attributes, including growth form, successional status and tree size.

Table 3. Classification of forest landscape types in tropical forest area of Hainan Island, South China

Vegetation type	Disturbance regime	Time of recovery (year)	Landscape type	Code	No. Plots	Plots size (ha)
Lowland rainforest	Selective logging	Early stage (<15)	Early-successional selective logged lowland rainforest landscape	LT1	10	0.40
	Clear cutting	Early stage (<15)	Early-successional clear cut lowland rainforest landscape	LT2	9	0.36
		Middle stage (52–60)	Mid-successional clear cut lowland rainforest landscape	LT3	6	0.24
	Undisturbed	Late stage	Old-growth lowland rainforest landscape	LT4	20	0.80
Montane rain forest	Selective logging	Early stage (<25)	Early-successional selective logged montane rainforest landscape	LT5	21	0.84
		Middle stage (25–45)	Mid-successional selective logged montane rainforest landscape	LT6	22	0.88
	Undisturbed	Late stage	Old-growth montane rainforest landscape	LT7	30	1.20
Tropical coniferous forest	Undisturbed	Late stage	Old growth tropical coniferous forest landscape	LT8	17	0.68

First we distinguished two types: the shrubs group and the trees group, based on growth form. Then we subdivided the two groups into the following three types: the early-successional group, the mid-successional group and the late-successional group. The tree species at the early-successional status tended to build low-density stems because of fast growth, in contrast to those species with higher wood density at the later-successional status because of slow growth (Peter et al. 2000; Verburg and van Eijk-Bos 2003). In addition, there is a positive correlation between wood density and seed mass (Ter Steege and Hammond 2001). The wood density and the seed mass play prominent roles in determining the successional status of woody species. The seed sizes of various species were collected from the references, and there were more data than the seed mass. Because of close correlation between the seed mass and the seed size (more detail in discussion), we applied the seed size to analyze the successional status for each individual tree species. As was done by Peter et al. 2000, apart from those typical pioneers (defined as the early-successional group in the present study), we classified the wood density into three levels: light (0.12–0.49 g/cm^3), medium (0.49–0.80 g/cm^3), and heavy (0.80–1.02 g/cm^3). In addition we set up three seed classes: small (0.30–9.0 mm), medium (9.0–20.0 mm) and large (20.0–59 mm). The species with light, medium wood and small, medium seeds were grouped together for mid-successional groups and species with heavy wood and large seeds for late-successional groups. In a few cases, the successional status of some species without explicit data was determined using additional information on successional behavior from local experienced botanist (Yang XS, pers. comm. 2005). Tree-fall gaps created by giant gap-forming trees profoundly affects the dynamics of both communities and populations within tropical forest (Gray and Spies 1996; Jiang and Zang 1999; Runkle 2000; Miura et al. 2001; Zang et al. 2001). The abundance, diversity, and canopy characteristics of those giants may have effects on canopy and stand turnover rates as well as the heterogeneity of light environments within the tropical forest (Denslow 1996; Laurance 2000). Therefore we separated those emergent and canopy trees as a single group in which trees species were defined by canopy size (>100 m^2) and DBH (>30 cm). Finally, we constructed seven functional groups: early-successional shrub species (F1), mid-successional shrub species (F2), late-successional shrub species (F3), early-successional tree species (F4), mid-successional tree species (F5), late-successional tree species (F6), and emergent and canopy tree species (F7).

Data analysis

Nomenclature of family, genus, species, and growth forms followed *Flora Hainanica* (Chun 1964, 1965; Guangdong Institute of Botany 1974, 1977). Data on the wood densities, seed masses and seed sizes of studied species were collected from published literature including Chun (1964, 1965); Joint Working Group on Hainan Timber Research (1966) and State Forestry Administration (2001). These data provided information on wood density, seed size and seed mass for 359, 351 and 189 tree species for this study, respectively. The wood densities ranged from 0.12 g/cm^3 to 1.02 g/cm^3. The seed sizes were between 0.3 mm and 59 mm. The seed masses varied largely from 0.05 g per one thousand seeds to 9 180 g per one thousand seeds. To exclude an area size effect, species richness and stem abundance were represented by the number of species and the number of individuals of all species per 400 m^2 plots for each forest landscape. The size of canopy was attained with an ellipse area formula. The nonparametric χ^2 test was used to determine whether family, genus, and species had equal frequency distribution among functional groups. We also examined differences in species richness and stem abundance between functional groups in each forest landscape type using non-parameter Kruskal-Wallis test. One-way ANOVA with repeated measurements was used to test for statistical differences in species richness and stem abundance of each functional group among different forest landscape types over time. Prior to the statistical analysis, all data were rank transformed. When equal variance was assumed, the method of least significant difference (LSD) was applied ($P < 0.05$). When equal variance was not assumed, the Games-Howell method was used ($P < 0.05$). The relationship between species-specific seed size and wood density was determined with Pearson correlation tests. Statistical significance was tested at $\alpha = 0.05$. All analyses were carried out with SPSS 13.0 (SPSS Inc., 2004, Chicago, IL, USA).

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