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Traditional forest management has limited impact on plant diversity and composition in a tropical seasonal rainforest in SW China

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ABSTRACT

In order to determine the impacts of different traditional forest management types on plant diversity of the seasonal tropical rainforests and infer effective conservation strategies, four types of forests with different management histories were studied in Nabanhe National Nature Reserve (NNNR), Xishuangbanna, China. They were: old-growth forest (non-timber product collection allowed), understorey planted old-growth forests, old secondary forests (~200-years after slash and burn), and young secondary forest (15–50-years after slash and burn). Although human activities affected tree diversity and composition of the forests in NNNR, the forest regeneration potential of the different management systems were good. Even the young secondary forests, that showed the lowest Fisher's alpha diversity at the plot level, had similar diversity levels to old-growth forest when all plots were combined. Number of red list tree species, timber species, and edible plant species in young secondary forests was as high as those of old-growth forests, and higher than old secondary forests. Additionally, there were a number of vulnerable and endangered species that were more common in the secondary than old-growth forests, indicating the high conservation value of secondary forests. Understorey plantation in old-growth forest, however, impaired regeneration of the climax species. The beneficial effects of traditional forest use depend strongly on its small scale and its close proximity to undisturbed forest, which serves as a species source during secondary forest regeneration. Unfortunately, traditional forest use is now under serious threat by expanding large-scale monoculture rubber plantations.

1. Introduction

Due to rapid human population growth, pressure on natural ecosystems has increased dramatically during the past 50 years (Potts, 2007), and half of the remaining tropical forests are already degraded old-growth forests and secondary forests (ITTO, 2002; FAO, 2007). Many studies have focused on the influence of human disturbance on species diversity and composition of forests (e.g. Cannon et al., 1998; Slik et al., 2002; Meijaard et al., 2005; Chapman et al., 2010). These studies show that human activities influence forest plant diversity in different ways depending on the severity and type of disturbance (Putz et al., 2000; Zhu et al., 2007). Also, disturbance impacts tend to interact with natural environmental habitat factors, such as soils, topography, and climate (Potts et al., 2002; Testi et al., 2009). Knowledge of the response, resilience, and regeneration of degraded old-growth forest and secondary forests after disturbance has attracted increasing attention because of the growing importance of these forest types for species conservation in the tropics (Chazdon et al., 2009b). And since tropical forests are relatively poorly understood compared to temperate forests (Chazdon, 2003), information regarding influences of different types of human disturbances is urgently needed for developing effective conservation strategies in the tropics (Chazdon et al., 2009a).

Many tropical forests previously thought to be old-growth forests were found to be exposed to traditional land use systems in the past (Bush and Colinvaux, 1994; Clark, 1996; Bush et al., 2007; Kennedy and Horn, 2008). Therefore, the current forest structure and composition may reflect the impacts of former land use history, and disturbances in the distant past should be considered in tropical forest research and management (Chapman et al., 2010). Determining the impacts of traditional land use types on tropical forests is necessary for understanding the relative contribution of historical land use in current forests. In addition, although it is still a point of discussion whether the livelihood

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development of local people should be integrated into the conservation of native ecosystems (Redford and Sanderson, 2000; Sunderland et al., 2008), some studies showed that traditional forest management by local villages in Europe and Canada was sustainable and beneficial for biodiversity conservation (Berkes and Davidson-Hunt, 2006; Elbakidze and Angelstam, 2007; Scotti and Cadoni, 2007). The impacts of traditional land use by local people in tropical forests, however, are poorly understood, and more scientific understanding is required.

The traditional land use systems in the tropics of Southeast Asia have been under big threat of rapidly expanding rubber plantations (Guo et al., 2002; Zhu et al., 2004; Li et al., 2006; Fu et al., 2009; Qiu, 2009; Ziegler et al., 2010) and oil palm plantations (Donald, 2004; FAO, 2007; Koh and Wilcove, 2008; Scharlemann and Laurance, 2008; Sodhi et al., 2010), which severely threaten the biodiversity in this region (Sodhi et al., 2010). As a part of the SE Asian tropics, Xishuangbanna is located at the northern limit and has a seasonal climate (Cao et al., 2006). The tropical forests in this region are floristically similar to the rain forests from the lower latitude seasonal tropics of SE Asia (Zhu et al., 2006; Zheng et al., 2006). Xishuangbanna harbors 16% of the plant diversity of China (Liu et al., 2002), and is included in the Indo-Burma diversity hotspot (Myers et al., 2000; Cao et al., 2006). However, In spite of the importance of the biodiversity of this region and the big threat imposed by human activities, the impacts of different types of traditional human disturbance on the diversity and composition of forest ecosystems in Xishuangbanna is relatively little studied, even though such research is urgently needed for developing effective conservation strategies.

The objectives of our study were (1) to determine the impacts of different traditional human forest use types on the forest structure and species composition of tropical seasonal rainforests in Nabanhe National Nature Reserve, as well as assess their conservation potentials, (2) to understand the succession pattern of tropical seasonal rainforest after disturbance. A total of twenty plots in four forest types (five plots per forest type) with a different management/disturbance regime were included in this study: (i) old-growth forest that was open to understorey non-timber products collection, (ii) old-growth forests with understorey *Amomum* plantation, (iii) old secondary forests about 200-years after slash and burn, and (iv) young secondary forest about 15–50-years after slash and burn. The relationships between forest management types, environmental factors, plant diversity and plant species composition were examined, and implications for effective conservation strategies in the tropics were discussed.

2. Materials and methods

2.1. Research area and plot setting

Nabanhe National Nature Reserve (NNNR) is situated in Xishuangbanna, Yunnan province, China (22°04′–22°17′N; 100°32′–100°44′E) (Fig. 1). The Reserve protects a watershed area of 21,100-ha surrounded by hills and mountains, which range in altitude between 539 m and 2304 m. Annual rainfall varies from 1200 mm to 1700 mm. However, 81–95% of the rainfall occurs in the rainy season, which lasts from May to October (NNNR Bureau, 2006). Annual mean temperature varies between 18 and 22 °C. The core zone of the National Reserve covers 3900 ha, the buffer zone covers ca. 5800 ha, and the experimental zone covers ca. 11,400 ha. Nabanhe was designated for the protection of its fauna

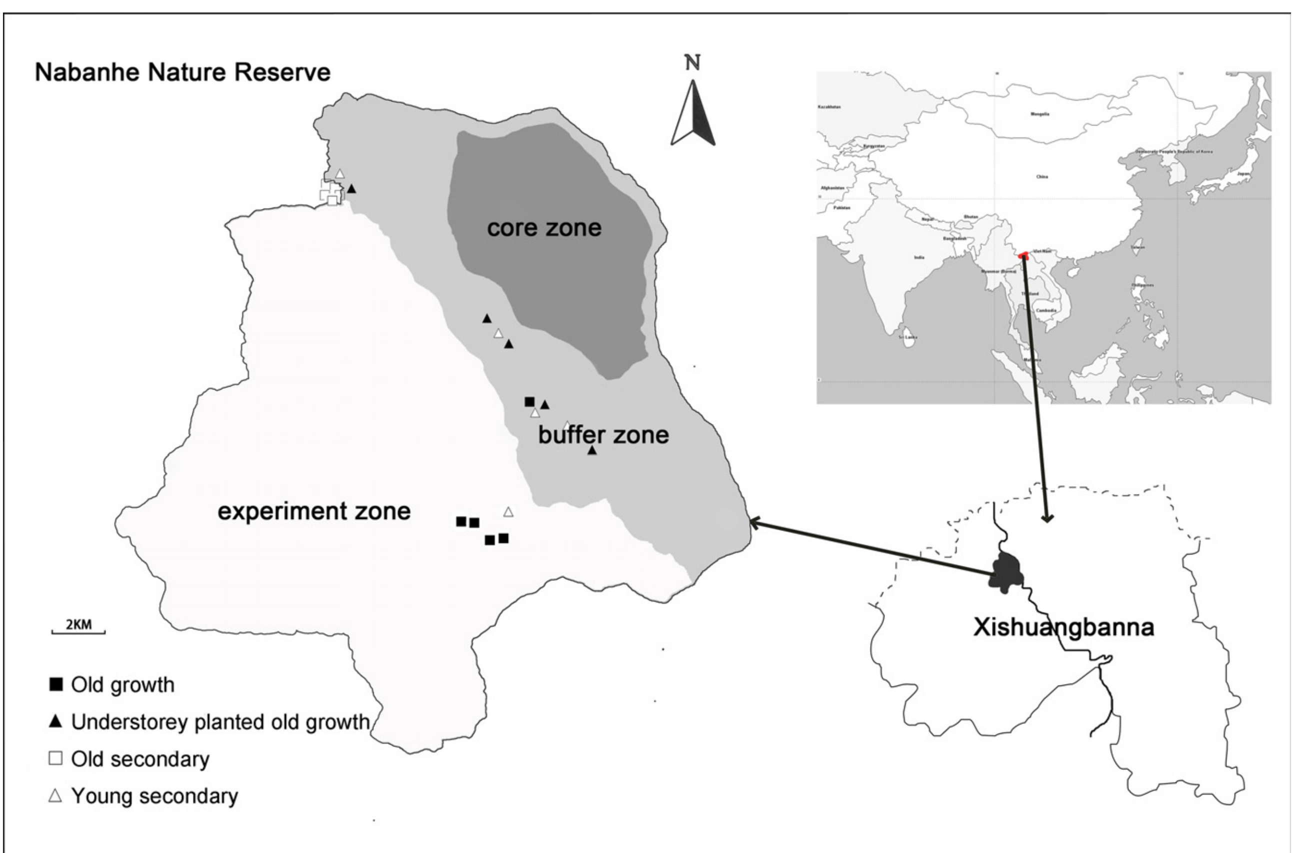

Fig. 1. Map of the Nabanhe National Nature Reserve. Locations of the 20 plots are indicated as follows: open squares indicate old secondary forest, closed squares represent old-growth forest, open triangles represent young secondary forest, and closed triangles represent forest with *Amomum villosum* plantation in the understorey.

in 1979, and then changed to a local Nature Reserve status in 1991 and after that to a National Reserve status in 2000. In a previous study in Nabanhe, 1780 vascular plant species were recorded, belonging to 820 genera and 171 families (Tao, 1989). There are six main vegetation types in Nabanhe: (1) tropical seasonal rain forest (mainly distributed in valleys along the Nabanhe river basin below an elevation of 900–1000 m), (2) tropical montane evergreen broad-leaved forest (the main vegetation type in the mountain areas above 1000 m elevation), (3) deciduous broad-leaved forest, (4) warm coniferous forest, (5) bamboo forest and (6) shrub lands (Tao, 1989; NNNR Bureau, 2006; Zhu, 2007). The present study focused on the influences of traditional land uses on typical tropical seasonal rain forests, which are quite different from the other forest types in community physiognomy and species composition (Tao, 1989; Zhu, 2007).

For this study we established a total of 20 plots in four different traditional forest management types (five plots each; Fig. 1), as listed in the introduction. The historical forest use by local people includes collecting non-timber products (mainly understorey or epiphytic herbs, fruits and mushrooms for food and medical use) from the old-growth forests, and slash and burn, which burned the old-growth forests for agricultural use and then abandoned the land after about 7–8 years of use. The land was then left for natural succession. Young secondary forests, and old secondary forests selected for this study have been left for natural succession for 20–50 years, and about 200 years, respectively. Within this time, slash and burn was not repeated. Some forests recognized as holy mountain forests (in small size) were never burned for agricultural use because of religious reasons. Slash and burn based agriculture usually only allows the food supply for the family and very little extra income could be generated. The understorey planting of ginger *Amomum villosum*, whose seeds are widely used in Chinese medicine, was promoted by the government in 1970s to improve the local peoples income. Understorey planting of ginger was then favored by local people because of its high income generated. However, rubber plantation is more favored by local people in recent years due to the continuing price increase of rubber in local and international markets. Ages of the plots were determined by questioning local people from villages near each plot. Efforts have been made to allocate the plots evenly along the valley, and to cover most of the distribution area of tropical seasonal rain forest in the reserve. However, the old-growth forest plots were relatively close to each other (also the old secondary forest plots) because of the limited distribution of these two forest types in the reserve. Most remaining forest in the reserve has been converted to *Amomum* understorey or rubber plantations.

2.2. Plant inventory and environmental variables measurement

In the 20 plots (25 × 20 m, except for the old secondary forest where plots were 10 × 50 m because this forest was located in narrow valleys), all trees with a diameter at breast height (dbh) ⩾ 5 cm were identified and their diameter measured. Most previous analyses in Xishuangbanna used the 20 × 25 m plot shape (e.g. Zhu et al., 2005; Shi and Zhu, 2009). Following the plot design in this area allows further analysis combining our data with the data from other forest areas in this region. Longer plots (10 × 50 m) used in narrow valleys will capture more beta-diversity and landscape variability, so they might overestimate diversity a bit. However, the effect is probably very limited because of the small plot size. Tree heights were estimated visually. Large woody climbers, vine species and their abundance level (1–7 indicate low to high abundance) were also recorded in the plots. Treelets (with a dbh < 5 cm), seedlings, shrub and herb species were identified in five 2.5 × 2 m subplots (four corners and the center) within each 500 m^2 plot. Vouchers were collected for plant species that could not be identified in the field and were deposited in the Herbarium of Xishuangbanna Botanical Garden, CAS, Menglun, Yunnan, China.

GPS-coordinates and elevation were logged with a GPS receiver in the middle of each plot. For each 500 m^2 plot, using a 1:50,000 contour map, we estimated the slope. Using a compass, the aspect was recorded as 1, 2, 3, 4, and 5 with 45° intervals starting from North to South. Topographic position of the plots were defined as 0 = flat bottom of valley, 1 = lower 30% of a slope, 2 = middle 30% of a slope, 3 = upper 30% of a slope, 4 = ridges and flat shoulders of mountain slopes.

2.3. Plant information collection

Commercial timber tree species in NNNR were determined using the Tropical Timbers of the World (Chudnoff, 1984) and the Flora of China (www.hua.huh.harvard.edu/china). Non-timber useful plant species (for livelihood of local people or commercial use) were identified based on previous ethnobotanical studies in NNNR (Yin, 1989; Zhang and Wu, 2004). Red list species in Nabanhe National Natural Reserve were based on the *China plant red data book–Rare and endangered plants* (China National Environmental Protection Agency and Institute of Botany, Chinese Academy of Sciences, 1992), and the *Rare Plants of Yunnan in China* (Gong et al., 2006). Late or early-successional species classification was based on long-term monitoring of the succession dynamics of species in the forests (both old-growth and secondary forests) in this region (Lin, 2007; Lin and Cao, 2009) and the information available in the Flora of China.

2.4. Data analysis

Species-individual curves show the relationship between number of species and number of individuals. Species-individual curves were generated by program EstimateS (v. 7.5; Colwell, 2005). To generate species-individual curves of the 20 plots, individuals recorded in each plot were randomly sorted and the species number accumulation was tallied 50 times to get the mean value. This analysis was repeated for all individuals within each forest type to construct the species-individual curves of the four studied forest management types.

For each plot the density of large trees (dbh ⩾ 10 cm), density of small trees (5 ⩽ dbh < 10 cm), species number of larger trees (dbh ⩾ 10 cm), and species number of small trees (5 ⩽ dbh < 10 cm) were calculated to represent the structure of the forest. Fisher's alpha was calculated according to Fisher et al. (1943) to determine overstorey tree diversity, while Chao2 was calculated according to Chao (1987) and used to examine the understorey tree diversity. Timber tree density, species number and basal area, together with number of red list species and number of useful plant species were used to examine the conservation value of the different types of forests. One-way ANOVA analysis with a post hoc Least Significant Difference (LSD) test was used to check whether those variables were different among the four forest types. When, even after data transformation, unequal variances were detected between the four forest types for a test variable (which violates the basic assumptions for running an ANOVA), a non-parametric Kruskal–Wallis test was used instead.

Abundance of late-successional trees in overstorey (individual number), percentage of late-successional trees in the overstorey (%), frequency of late-successional trees in the understorey, proportion of late-successional trees in all tree in understorey (%) were calculated to examine the succession status of the forest after different types of disturbance. One-way ANOVA with LSD post hoc test was used to check whether those variables were different among the four forest types. Rank transformation was used to correct data if homogeneity of variance was not satisfied.

A Canonical Correspondence Analysis (CCA) was used to evaluate which habitat variables best explained the differences in species composition among the plots. Overstorey and understorey were separated in the CCA analysis because human disturbance types and severity were different in these two forest layers and because data were collected differently in these two vegetation layers. For example, understorey thinning and planting as practiced in the *Amonum* forests disturbs the understorey but has little direct effect on species composition of the overstorey. The CCA analysis was done with Multi-Variate Statistical Package (MVSP; Kovach Computing Services), using the abundance matrix of tree species in the plots for overstorey species and the species frequency matrix for the understorey species. Longitude, latitude, elevation, aspect, slope, topographic position, the nearest distance to a plot of the same type, basal area, canopy height, vine abundance and liana abundance were included as environmental variables.

3. Results

3.1. Plant inventory

A total of 1069 trees, 195 tree species (dbh $\geqslant$ 5 cm), 52 liana species, and 15 vine species were recorded in the overstorey of the 20 plots. Additionally, a total of 337 species were recorded in the 100 understorey subplots. This included 147 tree species (41 of which were not found in the overstorey), 14 fern species, 59 herb species, 56 shrub species (nine scandent or climbing shrub species included), 17 vine species, and 43 liana species. There were 118 late-successional species in these forest communities compared to 100 early-successional species. Forty-five species (including 39 early-successional species) were unique in young secondary forests, which was a factor 2–3 higher than the numbers found in the other three forest types.

3.2. Species-individual curve

All four forest management types showed remarkably similar species accumulation curves when all plots within a forest type were combined, as suggested by the overlap of 95% confidence envelops (Fig. 2A). Only when the separate plots were analyzed (Fig. 2B) the young secondary forest plots showed markedly lower species accumulation (the 95% confidence interval did not overlap with those of other types; data not shown).

3.3. Forest structure, diversity and conservation index

Tree species number and tree volume did not differ across the forest types (Table 1). Tree height and DBH was lower in young secondary forests, while other types of forests did not show differences (Table 1). Tree densities ranged from 36 to 72 trees per plot (Table 1), and differed significantly between the forest types, with significantly lower densities of large trees in old secondary forest and significantly lower density of small trees in the understorey planted forest (Fig. 3A and B). Total basal area was smallest in the young secondary forests (Fig. 3E). Large tree species density showed a progressive decline from old-growth to understorey planted to old secondary to young secondary forest (Fig. 3C). Fisher's alpha was only significantly lower in young secondary forest (Fig. 3F). For small trees, the species density was lowest in the understorey planted forest because of the low overall tree density (Fig. 3D).

Late-successional species were most abundant in old-growth forest and lowest in young secondary forest (Fig. 3I), but as a percentage of stems they were only less common in the young secondary forest (Fig. 3J). This pattern was similar for the forest understorey (Fig. 3K and L). On the other hand the abundance of

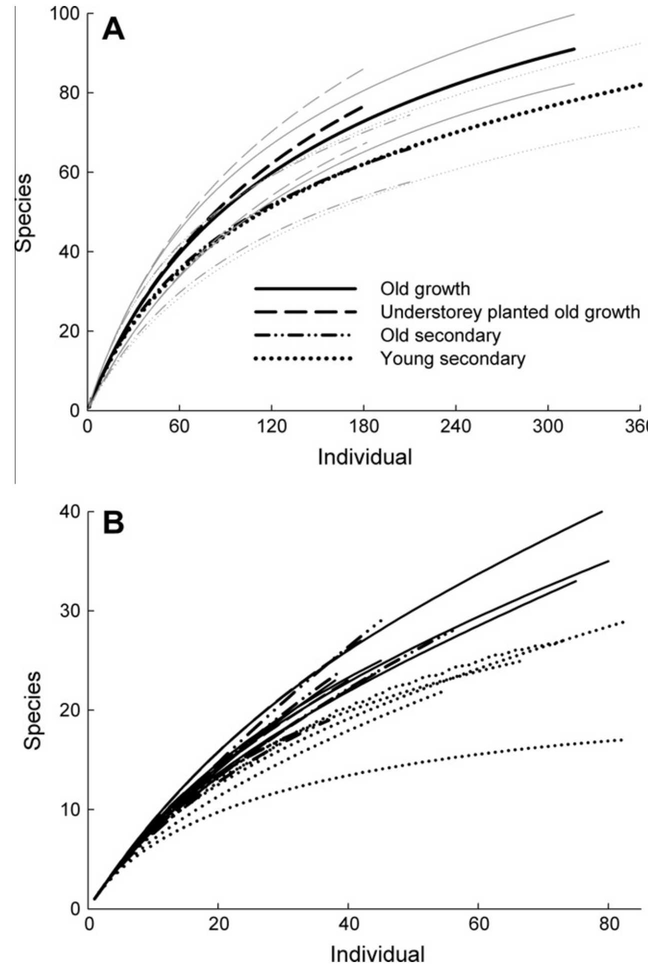

Fig. 2. Species-individual curves: (A) all plots per forest type combined, and (B) the 20 individual plots. Solid lines indicate old-growth forest, dash-dash represents old secondary forest, dash-dot-dot represents forest with *Amomum villosum* plantation in the understorey, and dotted lines represents young secondary forest. Lines in grey indicate 95% confidence envelopes.

timber trees was highest in the young secondary forest (Fig. 3G), while non-timber useful plants were most common in old-growth forest and least in the old secondary forest (Fig. 3H). We found no significant differences in the other measured variables (results not shown). Though no significant difference was found in number of red list trees among different types of forests, the composition of red list trees from secondary forests was different from those in old-growth forests (Table 2).

3.4. Multivariable analyses

The first axis of the CCA based on overstorey species composition explained 13.9% of data variance while the second axis explained 9.8%. For the CCA based on understorey species composition the first and second axes explained 13.7% and 11.0%, respectively. The first axes of especially the overstorey and to a lesser extent the understorey CCA were mainly related to human disturbance and forest successional variables (basal area, canopy height, vine abundance) (Fig. 4A and B). Aspect and topographic position also relate to disturbance as people mostly selected top slope positions and south facing sites for agriculture. The second CCA axis of the overstorey and to a lesser extend the understorey analysis was mostly determined by environmental and spatial variables (elevation, latitude, longitude). The first axis of the overstorey CCA mainly separated the young secondary forests from the

Table 1
Average tree species number, tree density, tree height, DBH, and volume of different types of forests. Values are means ± SE. Letters followed by same letter did not differ significantly ($P > 0.05$).

	Tree species (per plot)	Tree density (per plot)	Tree height (m)	DBH (cm)	Volume (m^3)
Old-growth	31 ± 3a	63 ± 9ac	17 ± 2ab	29 ± 5a	72 ± 22a
Understorey planted old-growth	22 ± 2a	36 ± 3b	21 ± 1a	39 ± 5a	89 ± 16a
Old secondary	24 ± 2a	42 ± 4b	16 ± 1ab	33 ± 4a	64 ± 21a
Young secondary	24 ± 2a	72 ± 5c	13 ± 2b	16 ± 2b	21 ± 9a

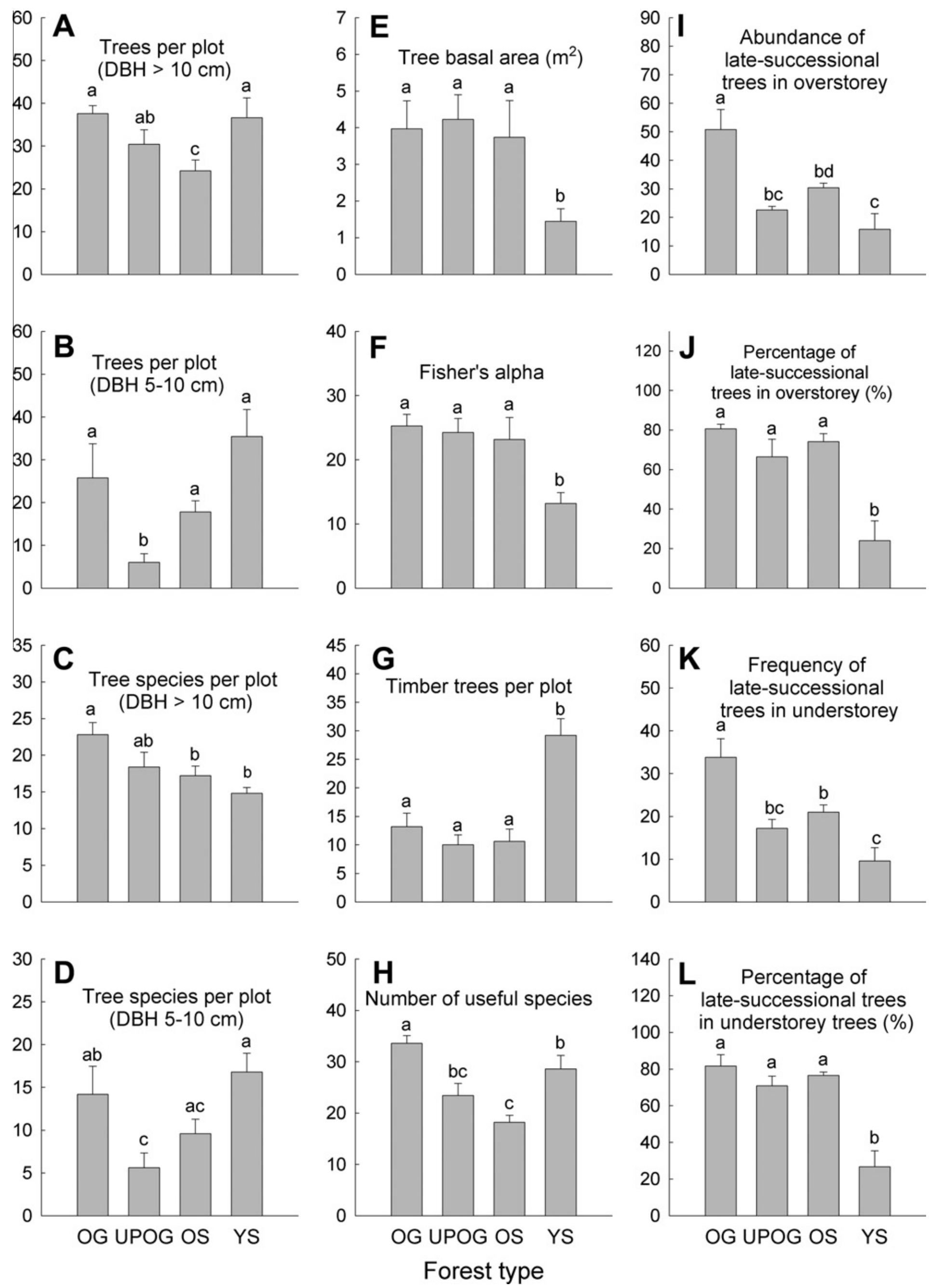

Fig. 3. Density of large trees per plot (dbh>10 cm) (A), small trees per plot ($5 \leqslant dbh \leqslant 10$ cm) (B), species number of large trees (dbh > 10 cm) (C), species number of small trees per plot ($5 \leqslant dbh \leqslant 10$ cm) (D), total tree basal area (E), Fisher's alpha (F), timber tree abundance (G), number of useful species (H; including understorey trees and herbs), abundance of late-successional tree species in overstorey (I), percentage of late-successional trees in all trees of overstorey (%) (J), frequency of late-successional trees in understorey (K), percentage of late-successional trees in understorey (%) (L). OG represents the old-growth forest; UPOG represents the understorey planted old-growth forest (the old-growth forests with *Amomum villosum* plantation in the understorey); OS represents old secondary, YS represent young secondary. Bars are means + standard error (SE). Bars topped by different letters differ significantly ($P < 0.05$).

other three forest types, while the second axis separated the old secondary forest from old-growth and understorey planted forest (Fig. 4A). The analysis shows that understorey planted forest is most similar to undisturbed forest in overstorey species composition and abundances. A similar pattern was found for the forest understorey tree species composition (Fig. 4B), with young second-

Table 2
Red list species found only in old-growth forests, only in secondary forests, and in both types of forests (shared species). The categories in the status column refer to the national or provincial protected plant species categories, classified based on conservation values (category I has the highest conservation value).

Species	Family	Status
Old-growth only		
Myristica yunnanensis Y.H. Li	Myristicaceae	Endangered
Pterospermum menglunense Hsue.	Malvaceae	Endangered; National Category II
Toona ciliata Roem.	Meliaceae	Vulnerable; National Category II
Antiaris toxicaria Lesch.	Moraceae	Rare
Cyclobalanopsis rex (Hemsl.) Schott.	Fagaceae	Rare
Secondary only		
Litsea pierrei Lec.var. *szemois* Liou.	Lauraceae	Endangered
Toona ciliata var. *pubescens* (Fr.) Hand-Mazz.	Meliaceae	National Category II
Dalbergia fusca Pierre	Fabaceae	Vulnerable; National Category II
Mangifera sylvatica Roxb.	Anacardiaceae	Vulnerable; National Category II
Paramichelia baillonii (Pierre) Hu	Magnoliaceae	Vulnerable; National Category II
Acrocarpus fraxinifolius Wight ex Arn.	Fabaceae	Rare
Shared species		
Horsfieldia tetratepala C.Y. Wu	Myristicaceae	Endangered
Horsfieldia pandurifolia Hu	Myristicaceae	Vulnerable
Pometia tomentosa (Bl.) Teysm. et Binn.	Sapindaceae	Vulnerable
Alseodaphne petiolaris (Meissn.) Hook. f.	Lauraceae	Provincial Category III
Amoora yunnanensis (H.L. Li) C. Y. Wu	Meliaceae	Provincial Category III

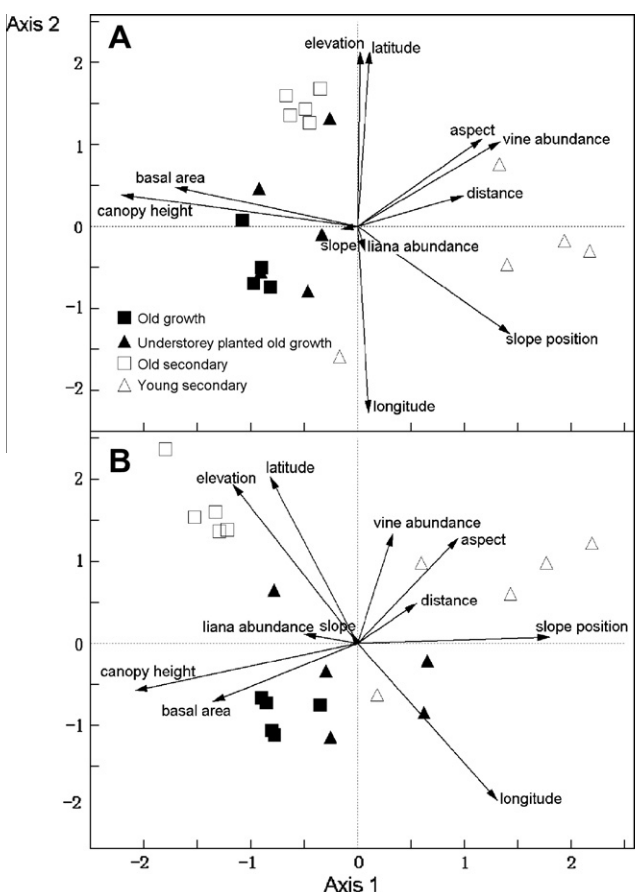

Fig. 4. Ordination diagram of the Canonical Correspondence Analysis (CCA) showing the plots and environmental variables for overstorey (A) and understorey (B). The first axis in overstorey CCA explains 13.9% of the data variance while the second axis explains 9.8%. The first and second axes in the understorey CCA explain 13.7% and 11%, respectively. "Distance" represents the distance to the nearest plot of same forest type. Open squares represent old secondary forest, closed squares represent old-growth forest, open triangles represent secondary forest, and closed triangles represent forest with *Amomum villosum* plantation in the understorey.

ary forest separated from the other forest types along the first CCA axis, while old secondary forest was separated along the second CCA axis.

4. Discussion

4.1. Impacts of traditional forest use

Although slash and burn dramatically altered forest structure and species composition in NNNR, the forest recovered quickly in structure and plant diversity. Young secondary forests showed similar tree density and a closed canopy when compared with old-growth forests, although basal area was still about 75% lower. This fast recovery of stem density was, like in other tropical forests (Samejima et al., 2004) caused by the quick establishment of early successional tree species. Young secondary forests had significantly lower Fisher's alpha indicating a high ratio of individual to species number resulting from high tree abundance and dominance of some early successional tree species. In spite of the relatively low Fisher's alpha diversity at the plot level, young secondary forests had high diversity when all plots were combined, indicating high beta-diversity.

Although forest structure and, to a lesser extent, plant diversity recovered quickly, tree species composition recovery proceeded very slowly, with the 200 year old slash and burn forests in our study area just approaching the species composition found in old-growth, undisturbed forest. These 200-year-old secondary forests showed similar tree abundance and equally big basal area compared to old-growth forest, whereas the abundance of late-successional species in overstorey, and frequency of late-successional species in understorey were still significantly lower than that of the old-growth forest. Therefore, our results agree with several studies in the tropics that show slow recovery of tree species composition after severe disturbances (Chapman et al., 2010). The fast recovery of forest structure and biodiversity in the early phases of forest succession is mainly due to the fast influx and establishment of early-successional species, which also explains the big difference in species composition between old-growth and secondary forest types. The later stage of succession is characterized by re-establishment of late-successional species which is usually slow due to limited seed dispersal capabilities of late-successional species, absence of some seed dispersers in secondary forest, and unsuitable micro-habitat regimes including differences in the herbivore community/density in secondary forests (Barlow et al., 2002; Fredericksen and Fredericksen, 2002; Slik and van Balen, 2006; Slik et al., 2008).

Another typical traditional forest use type in NNNR, plantation of *A. villosum* in the understorey, did not influence the species composition nor basal area of the overstorey. However, density and frequency of late-successional trees in the understorey was much lower in understorey planted forests than in old-growth forests because of the active thinning of understorey woody plants for *Amomum* cultivation. Therefore the regeneration of the climax species could be impaired in the long term if the thinning of understorey woody plants continues, making it an unsustainable way of forest management for biodiversity protection. Although the regeneration has been impaired, understorey planted forests still hold sufficient species in the overstorey that can act as seed source for regeneration and recovery, which will occur once the understorey thinning stops. Therefore, with relatively little effort, a better management policy aimed at sustainable use of the forest with respect to biodiversity could be implemented by designing a mosaic of understorey thinning/planting combined with areas where the forest understorey is left in peace (Gao and Liu, 2003).

The limited impacts of traditional forest use on tree diversity of the forests in NNNR may result from the fact that these tropical forests have a long history of human occupation and disturbance, and current species compositions might already reflect that, even in old-growth forests (Fairhead and Leach, 1998; Chazdon, 2003). Additionally, Asia's tropical forests are subject to frequent natural disturbances including El Niño-related droughts (Haberle and Ledru, 2001; Slik, 2004; van Nieuwstadt and Sheil, 2005), flash floods, wind throws, landslides, tree falls (e.g. Proctor et al., 2001; Pitman et al., 2005; Restrepo and Alvarez, 2006), and fires (Baker et al., 2005; Cochrane, 2003). Thus, the term old-growth forest in the Asian seasonal tropics might be misleading since these forests are actually quite dynamic.

4.2. Potential benefits of traditional forest use

Traditionally managed forests increased rather than decreased landscape level tree diversity in our study area, and secondary forests complemented rather than decreased diversity. Some studies suggest that although secondary forests, for example after logging, can exhibit high plant diversity, the conservation value is not that high (Fredericksen and Mostacedo, 2000; Pinard et al., 2000; Eichhorn and Slik, 2006). However, the secondary forests in NNNR showed comparable high stem and species numbers of red list trees, useful species (edible, medical and fiber plant, for livelihood of local people or commercial use), and timber trees. Forty-five tree species were unique in young secondary forests, which is two to three times higher than the numbers found in the other forest management types. Six red list species that appeared in the secondary forests were not found in the old-growth forests, and the timber species in the secondary forests were also very different from those in the old-growth forests. One of the most important and precious timber species in Xishuangbanna (Ye et al., 1999), *Dalbergia fusca*, was only found in secondary forests. Therefore, the secondary forests complement rather than decrease diversity and have their own unique position in plant species conservation not only because of their biodiversity, but also because of the high quality of the diversity. Rare and endangered species were also found in secondary forests by other studies (e.g. Zhu et al., 2007), and the importance of tropical secondary forests in biodiversity conservation has been recognized (de Jong et al., 2001; Chazdon et al., 2009b).

4.3. Environmental axis and limited distribution of old-growth forests

Human forest use generally changes environmental factors, such as light intensity, which will further influence the development of plant communities over time (Cannon et al., 1998; Uutera et al., 2000; Eichhorn and Slik, 2006). The present study showed that environmental factors also influenced human forest use with most young secondary forests being located at relatively low elevation, on mostly south faced flat upper or top slope positions (CCA results, Fig. 4). The CCA result also showed that minimum distance between plots has an impact on CCA axis 1, i.e. plots further apart are more different in species composition. Therefore the overall plant diversity of the old-growth forests and old secondary forests may have been underestimated in the present study because plots of these two types of forests were close together. Old-growth forest and old secondary forests may show higher species accumulation rate and total species numbers if the plots were located far away from plots within the same type. However, our plot setup was limited by the spatial distribution of remaining undisturbed and old secondary forests in Nabanhe National Nature Reserve due to the large expansion of rubber and *Amomum* understorey plantations. This signals the urgent need to preserve the remaining old-growth forest in this area.

4.4. Implications for conservation and forest management

Due to its high plant diversity and abundance of late-successional tree species, the old-growth forest serves as a seed source to facilitate the succession of the neighboring secondary forests and the early establishment of trees after slash and burn. Old-growth forests also hold many unique, endangered and vulnerable tree species that are rare or absent in secondary forests (Table 2). Therefor the conservation of old-growth forests with very limited distribution should be a priority. Our results showed relatively small impact of traditional forest use on forest structure, species composition and biodiversity, and even indicate potential benefits of traditional forest use by increasing landscape level diversity and species turnover. However, this beneficial impact of traditional land use is only possible when the undisturbed old-growth forests exist as seed source for succession. This system is now in danger of collapsing due to increasing human population levels, more intense forest use and especially the large scale clearance of forest for rubber monoculture in our research area (Guo et al., 2002; Zhu et al., 2004; Li et al., 2006; Fu et al., 2009; Qiu, 2009; Ziegler et al., 2010). For biodiversity conservation purposes, we like to stress the urgent need for research in looking for effective forest use strategies that intermix with protected secondary, old-growth forests, and forests managed for local people use so that an optimal balance between economic development and biodiversity conservation can be reached.

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