

Community assembly during secondary forest succession in a Chinese subtropical forest

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Abstract. Subtropical broad-leaved forests in southeastern China support a high diversity of woody plants. Using a comparative study design with 30 × 30 m plots ($n = 27$) from five successional stages (<20, <40, <60, <80, and ≥80 yr), we investigated how the gradient in species composition reflects underlying processes of community assembly. In particular, we tested whether species richness of adult trees and shrubs decreased or increased and assessed to which degree this pattern was caused by negative density dependence or continuous immigration over time. Furthermore, we tested whether rare species were increasingly enriched and the species composition of adult trees and shrubs became more similar to species composition of seedlings during the course of succession. We counted the individuals of all adult species and shrubs >1 m in height in each plot and counted all woody recruits (bank of all seedlings ≤1 m in height) in each central 10 × 10 m quadrant of each plot. In addition, we measured a number of environmental variables (elevation, slope, aspect, soil moisture, pH, C, N, and C/N ratio) and biotic structural variables (height and cover of layers). Adult species richness varied from 25 to 69 species per plot, and in total 148 woody species from 46 families were recorded. There was a clear successional gradient in species composition as revealed by nonmetric multidimensional scaling (NMDS), but only a poor differentiation of different successional stages with respect to particular species. Adult richness per 100 individuals (rarefaction method) increased with successional stage. None of the measured abiotic variables were significantly correlated with adult species richness. We found no evidence that rare species were responsible for the increasing adult species richness, as richness of rare species among both adults and recruits was independent of the successional stage. Furthermore, the similarity between established adults and recruits did not increase with successional stage. There was a constant number of recruit species and also of exclusive recruit species, i.e., those that had not been present as adult individuals, across all successional stages, suggesting a continuous random immigration over time.

Key words: BEF-China; chronosequence; detrended correspondence analysis (DCA); Gutianshan National Nature Reserve; immigration; negative density dependence; nonmetric multidimensional scaling (NMDS); permanent forest dynamic plots; random assembly; secondary forest succession; Zhejiang Province, China.

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INTRODUCTION

The last decades have much improved our understanding of the forces that affect tree species richness in forests. Local or community species richness, i.e., α -diversity, is increased by immigration and reduced by extinction, and both processes may be stochastic or deterministic (MacArthur and Wilson 1967, Hubbell 2001). While stochastic immigration mainly depends on the difference between regional species richness, i.e., γ -diversity, and α -diversity, and on the degree of dispersal limitation (Hubbell 2008), deterministic immigration additionally depends on the characteristics of the immigrating species, of the receiving community, and interactions between the two (Rejmanek 1996, Crawley et al. 1999, Mwangi et al. 2007). Stochastic extinction usually affects species with small population size (Simberloff 1988, Fischer and Stöcklin 1997, Matthies et al. 2004), whereas deterministic extinction may be due to environmental filtering (Lavorel and Garnier 2002) or exclusion of a plant species by competitors, pathogens, or herbivores (Schmid and Matthies 1994). An important mechanism acting against extinction is negative density or frequency dependence, which either occurs when negative interactions are less detrimental or positive interactions are more favorable among different species than among individuals of the same species (Wright 2002, Wills et al. 2006).

Interestingly, not much attention has been paid to the question of how stochastic and deterministic processes affect community assembly during secondary forest succession, although for a number of reasons such succession series are highly suitable systems for studying community assembly and diversity maintenance. First, some processes are directly observable, such as recruitment and mortality (Chazdon 2008). However, other processes such as the development of positive interactions are much less obvious, although it is generally assumed that they increase with time, as the ecosystems get more structured and more complex (Margalef 1963, Odum 1971). There is ample evidence for a temporal development of complementarity from biodiversity–ecosystem functioning (BEF) experiments (Tilman et al. 2001, Cardinale et al. 2007, Duffy 2009, Marquard et al. 2009), but not much is known from secondary forest succession series. Second, the general development of species richness along successional series is well known for many forest types (Howard and Lee 2003, Chazdon 2008). According to Howard and Lee (2003), four main patterns can be distinguished: species richness can monotonically decrease or increase with ongoing succession, peak at middle successional stages, or may not show any temporal trend. The absence of any trend might occur if changes in successional stages involve changes in environmental conditions to which only a limited but unpredictable number of species are adapted (Denslow 1980). While these patterns describe the net changes in species richness during succession, they do not discuss the underlying community assembly pro-

cesses, i.e., immigration and extinction dynamics. So far, it has not been analyzed to which extent the above-mentioned negative and positive forces act on net species richness during the course of secondary forest succession.

A continuous decrease in diversity during succession, caused by prevalence of extinction processes, is consistent with the hypothesis of initial floristic composition (Egler 1954). At the beginning of succession a large number of species immigrate, but more and more species go extinct as competition for increasingly depleted resources, mainly light, increases over time. In addition, stochastic extinction increases when individuals increase in size and the overall density of individuals declines. This sampling effect (Denslow 1995, Hubbell et al. 1999) also contributes to decreasing richness. In contrast, two major processes might promote an increase in tree species richness with successional age, resulting either in a monotonic increase or in a midsuccessional peak.

First, effects of negative density and frequency dependence, for example, Janzen/Connell effects (Janzen 1970, Connell 1971, Condit et al. 1992, Freckleton and Lewis 2006) might accumulate with time, and thus be more prominent in mature stands. Studying the diversity in subtropical and tropical forests in Queensland, Australia, Connell et al. (1984) called this effect compensatory recruitment, as it would compensate for the tendency of competitively stronger species to increase at the expense of weaker ones. Based on the observation that more common species had fewer seedling recruits per adult than rarer species, Connell et al. (1984) suggested that rare species were favored over common ones in terms of a per capita recruitment rate. Recently, Wills et al. (2006) compared the diversity of cohorts of different age and size in repeated census intervals of seven tropical forest plots. They found preferential establishment and survival of less abundant compared to more abundant species, which resulted in an increased enrichment of rare species with successional stage. As a consequence, rare species would be prevented from local extinction, and diversity would increase from the group of seedlings to the group including young and old trees.

Second, young successional stages might experience continuous immigration from late successional stages because those contain a considerable part of the regional species pool. Thus, young successional stages might start with a low number of tree species and then become enriched with time. Given a constant stream of immigrants from a random set of species, newly established cohorts would be expected to have a low floristic similarity to already established ones when the number of residents is low, such as in young stands. As succession progresses, composition of new cohorts would become increasingly similar to the established species, because more and more of the newly arriving species would already be present in the community (Anderson 2007). However, similarity between recruits

and the established trees might also reach local minima if there are clear successional stages that fundamentally differ in species composition (Chao et al. 2005).

In this paper, we ask whether tree species richness increases or decreases with increasing age of successional stages in a warm-temperate laurophyllous forest (hereafter called subtropical forest) in Zhejiang Province, China, and how stochastic or deterministic immigration and extinction may contribute to the net changes in species richness. These subtropical mixed forests are of particular interest for diversity research since they are similarly rich in woody species as tropical forests (Condit 1995, Wills et al. 2006, Legendre et al. 2009). In addition, they represent a formerly widespread ecosystem in South and East China (Wu 1980), which currently is under high pressure from intensive land use (Wang et al. 2007). Our motivation to address the impact of successional age on diversity originates from a recently initiated experiment that uses a large set of subtropical tree and shrub species in Jiangxi, China, close to the forest plots studied here, to explore the relationships between biodiversity and ecosystem functioning (*available online*).¹⁹ In the experiment, artificial stands with defined tree species diversity levels have been established by planting seedlings, and in consequence, during the first years, will only reflect the conditions of young successional stages with respect to microclimate, food web structure, and nutrient fluxes and pools. Thus, we were interested to learn to what extent young forest stands differ from old ones in all types of ecosystem functioning variables. This paper is the first contribution to this topic, asking how much tree and shrub richness and variables related to richness vary along a gradient of different stand ages. Our specific hypotheses were as follows.

1) Richness of tree and shrub species recorded on a fixed plot size is highest in young successional stages and decreases in the course of succession, mainly because of declining density of individuals. If the sampling effect is taken into account, i.e., if richness is corrected for a decreasing density of individuals in the course of succession, richness is expected to increase. In addition, we tested whether successional stage is a better predictor for species richness than other variables related to structure and site characteristics.

2) Rare species increasingly contribute to the potential effect of increasing richness with successional age. Under the assumption of a preferential survival of rare species, an increase in proportions of rare species should be less conspicuous in seedlings than in adult trees and shrubs. Consequently, a higher contribution of rare species should also be visible in a higher per capita recruitment success of rare species as compared to common ones as well as higher average per capita recruitment rates of plots containing a higher proportion of rare species.

3) In contrast to the former hypotheses, which are based on the assumption of a differential recruitment of common and rare species, we further hypothesized that establishment from a common recruitment pool could be a random process. Assuming continuous but random immigration, the richness of recruits should be constant over the different successional stages. However, given a limited regional species pool and increasing richness with successional time, the probability that species new to a plot would be among the recruits, i.e., those that are not yet present as adult individuals, should decrease in the course of succession. Likewise, the similarity in species composition between established adults and recruits is expected to decrease.

MATERIALS AND METHODS

Study site

The Gutianshan National Nature Reserve (NNR) is located in the western part of Zhejiang Province of China (29°8'18"–29°17'29" N, 118°2'14"–118°11'12" E; Fig. 1). The forest is representative of Chinese mixed broad-leaved forests (Wu 1980, Hu and Yu 2008, Legendre et al. 2009), with evergreen species dominating the forest in number of individuals (Yu et al. 2001), but with approximately similar proportions of deciduous species in terms of species number (Lou and Jin 2000). A total of 1426 seed-plant species of 648 genera and 149 families have been recorded as occurring naturally in the NNR. About 258 of the species are woody (Lou and Jin 2000). The Gutianshan NNR has an area of ~81 km², was initially established as a National Forest Reserve in 1975, and became a National Nature Reserve in 2001. The NNR comprises a large portion of broad-leaved forests of advanced successional stages (Hu and Yu 2008), which have not been managed since the beginning of the 1990s, as well as young successional stages and conifer plantations, mainly of the economically important timber species *Cunninghamia lanceolata* and *Pinus massoniana* (for authors of species names, see Appendix).

Most of the stands are secondary forests, evidenced by maximum tree ages of only 180 years, by the presence of relicts of agricultural terraces in almost all plots and by the presence of charcoal in almost all soil profiles. Within and adjacent to the Gutianshan NNR, extensive deforestation occurred during the Great Leap Forward in the 1950s, as in most parts of Southeast China. However, owing to very steep slopes, with some exceeding 30°, the Gutianshan area was only marginally usable for agricultural activities, and thus an exceptionally intact forest cover has been preserved.

The climate at Gutianshan NNR is warm-temperate with a short dry season in November and December and with warm summers. The climate conditions are characteristic of the subtropics with an annual average temperature of 15.1°C, January minimum temperatures of –6.8°C, July maximum temperatures of 38.1°C, and

¹⁹ (www.bef-china.de)

an accumulated temperature sum ($\geq 5^{\circ}\text{C}$) of 5221.5 degree-days per year.

Study design

Plots were randomly selected, stratified by successional age. In the following the plots are called Comparative Study Plots (CSPs). Different successional ages are the result of differences in elapsed time since the last forest harvesting, carried out manually by the local population for timber and firewood. Five successional stages were distinguished according to the age of the largest tree individuals in a plot, supported by additional knowledge of the last logging event in this part of the forest and local status as “feng shui” forest (1, <20 yr; 2, <40 yr; 3, <60 yr; 4, <80 yr; 5, ≥ 80 yr; see Plate 1). The plot assignment in the field was later confirmed by additional measurements of diameter at breast height (dbh) of all trees with >10 cm dbh in a plot, and of tree age, determined on 159 stem cores taken at breast height from 64 different tree species across all CSPs. CSP locations within strata were selected randomly; however, due to inaccessibility and extremely steep slopes ($>50^{\circ}$), parts of the NNR had to be excluded from sampling, thus resulting in an uneven spatial distribution of some of the plots (Fig. 1C). In total, 27 CSPs were established between May and July 2008. The number of plots per successional stage were 5 (<20 yr), 4 (<40 yr), 5 (<60 yr), 6 (<80 yr), and 7 (≥ 80 yr).

Species recording was performed between May and October 2008 with several visits per plot. Species names follow the nomenclature of the Flora of China (*available online*).²⁰ Each CSP has a size of 30×30 m on the ground. In horizontal projection this corresponded to an average area of 0.074 ha, close to the Chinese areal measure of 1 mu ($=0.067$ ha) and thus to the plot size used in the associated biodiversity–ecosystem functioning experiment at Xingangshan (Jiangxi Province, Fig. 1C). Soil moisture was assessed gravimetrically on soil samples taken from five depth increments (0–10, 10–20, 20–30, 30–40, 40–50 cm) in June/July 2008, November 2008, and March 2009. Here, we used mean values per plot by averaging the soil water contents over all depths and all dates. Soil samples for determination of pH, C, and N were taken in summer 2009 from nine locations in each plot at 0–5, 5–10, 10–20, 20–30, and 30–50 cm. The samples were pooled to form one bulk sample per CSP and depth interval, sieved (<2 mm) and air dried. Soil pH was measured potentiometrically in a 1:2.5 soil– H_2O suspension. Total C and N were determined on milled samples after heat combustion (1150°C) using Vario ELIII elemental analyzer (Elementar, Hanau, Germany). Since all soil samples are noncalcareous, the measured total C content equals organic carbon (C_{org}). In this paper only the topsoil (0–5 cm) data have been used, because these showed the highest variation among plots. A complete inventory of woody species (>1 m

height) was carried out in the entire plot. All herbaceous species and woody seedlings ≤ 1 m height (i.e., the seedling bank, hereafter called recruits) were recorded in a central subplot of 10×10 m on the ground. All individuals were identified to the species level, making use of herbarium samples and comparisons with correctly identified individuals, and counted per species. The proportion of unidentifiable individuals (>1 m height) in a CSP ranged between 0% and 2.3%. These individuals were not included in the subsequent data analysis. All measures in this paper are expressed per area on the ground (i.e., not converted to horizontal projection area).

Data analysis

We calculated the concentration of all species in one of the five successional stages, using the Phi value as a measure of fidelity, calculated with the Juice software (Chytrý et al. 2002). The Phi values were tested for significance by Fisher’s exact test, using a significance level of $P = 0.01$. At this level a species would be identified as being significantly characteristic of a successional stage if, for example, it occurred at least in three plots of this stage (assuming that the stage comprised 4–7 plots), but not in the other successional stages. The presence and absence of species in the different successional stages was used to calculate community turnover rates between successional stages according to Anderson (2007), defined as number of species that were either new to a successional stage or had disappeared, divided by the total sum of species in the preceding and subsequent successional stage. To analyze the floristic composition of all woody species we employed nonmetric multidimensional scaling (NMDS), using counts of individuals per CSP and Bray-Curtis dissimilarity. The statistics were computed with R (R Development Core Team 2008), using the vegan package (Oksanen et al. 2006). All 148 species of trees and shrubs with at least one individual >1 m in height were used in the analysis. Wisconsin double standardization, where species are first standardized by species maxima and then sites are standardized by site totals, was applied to square-root transformed abundance data. Default options were used for scaling, so that one unit means halving of community similarity from replicate similarity. Species scores were added as weighted averages. In a subsequent multiple regression, the NMDS plot scores on axes 1 and 2 were related to (1) variables describing plot characteristics (elevation, aspect, slope, geographical coordinates, height and cover of the different layers, coverage of bare ground, soil moisture, pH, C, N, and C/N ratio) and successional stage, and (2) to variables related to species richness (number of woody species and woody lianas [height >1 m] in the 30×30 m plot as well as number of herb species, woody recruit species [seedlings], woody climber species, and herb climber species in the 10×10 m

²⁰ <http://flora.huh.harvard.edu/china>

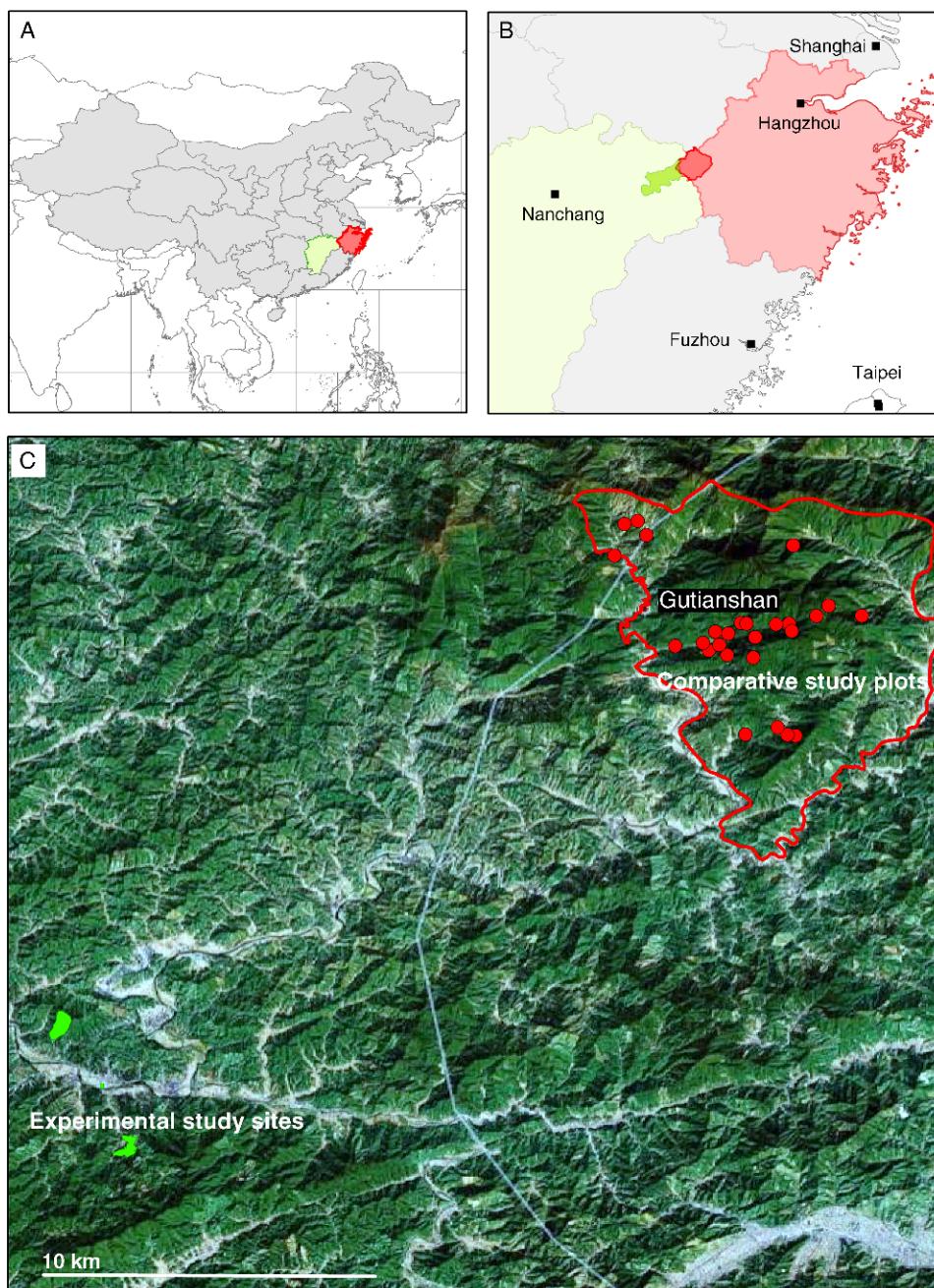


FIG. 1. Study area: (A) Zhejiang (red), and Jiangxi (green) Provinces; (B) Kaihua county in Zhejiang Province (red, area of Comparative Study Plots [CSPs] used for the study reported in this paper), Dexing county in Jiangxi Province (green, area where an associated forest biodiversity–ecosystem functioning experiment has been set up). (C) Gutianshan NNR (red line) with CSPs (red dots) in Kaihua county (Zhejiang Province) and the two associated experimental sites (green areas) in Dexing county, Jiangxi Province.

subplot [only recorded if height ≤ 1 m]). The significance of the correlations was assessed using permutation tests ($n = 999$). In addition, a detrended correspondence analysis (DCA) was performed to determine the gradient lengths and to yield an estimate of β diversity (Jongman et al. 1995).

All ordinary linear regressions with single predictors were calculated with R. A multiple regression was used to test the dependence of species richness of adult trees and shrubs (individuals >1 m height) on all variables describing plot characteristics and structure (for a list of variables, see Table 1A). The input variables were

TABLE 1. Correlation coefficients of (A) variables describing plot characteristics and structure and (B) variables describing species diversity of the different strata and life-forms with the first and second axis of the NMDS ordination.

Plot characteristics and richness variables	Abbreviation in Fig. 3	NMDS1	NMDS2	r^2	P
A) Plot characteristics					
Successional stage	Successional_stage	0.997	0.079	0.616	0.001
Age of the fifth-largest tree (yr)	Tree_age_max5	0.968	0.252	0.405	0.007
Elevation (meters above sea level)	Elevation	0.135	0.991	0.780	0.001
Location in the NNR (°N)	Coordinates_N	-0.143	0.990	0.319	0.012
Location in the NNR (°E)	Coordinates_E	0.947	0.320	0.395	0.003
Eastness = sin(aspect), with aspect in degrees	Aspect_E	-0.880	-0.475	0.185	0.095
Northness = cos(aspect), with aspect in degrees	Aspect_N	-0.572	0.820	0.075	0.413
Slope (°)	Slope	0.790	-0.613	0.047	0.555
Height of upper tree layer (%)	T1_height	0.985	-0.170	0.650	0.002
Cover of upper tree layer (%)	T1_cover	0.945	0.326	0.333	0.008
Height of lower tree layer (%)	T2_height	0.995	-0.098	0.557	0.001
Cover of lower tree layer (%)	T2_cover	-0.839	-0.544	0.130	0.170
Height of shrub layer (%)	SL_height	0.995	0.103	0.310	0.008
Cover of shrub layer (%)	SL_cover	-0.888	0.459	0.545	0.001
Cover of herb layer (%)	HL_cover	-0.428	-0.904	0.161	0.121
Bare ground (%)	Open_soil	-0.803	0.596	0.110	0.226
Soil moisture (g H ₂ O/g dry soil)	Soil_moisture	0.561	0.828	0.456	0.002
pH (0–5 cm) measured in H ₂ O	pH	-0.718	-0.696	0.201	0.070
Total carbon content, 0–5 cm (%)	C	0.691	0.723	0.332	0.007
Total nitrogen content, 0–5 cm (%)	N	0.724	0.690	0.390	0.003
Carbon/nitrogen ratio, 0–5 cm (% per %)	C_N	-0.553	-0.833	0.039	0.633
B) Richness variables					
Number of individuals of adult trees and shrubs (>1 m height)	N_individuals	-0.817	0.576	0.498	0.001
Number of adult tree and shrub species (>1 m height)	N_adult_species	1.000	0.011	0.183	0.091
Number of adult tree and shrub species (>1 m height) based on rarefaction with $n = 100$ individuals	N_adults_100	0.926	-0.378	0.421	0.004
Proportion of rare adult species	Prop_rare_adults	0.001	1.000	0.073	0.381
Proportion of deciduous adult species	Prop_decid_adults	-0.737	0.676	0.656	0.001
Number of adult climber species	N_adult_climber	0.363	0.932	0.015	0.839
Number of woody seedlings (≤1 m height)	N_recruit_species	0.166	-0.986	0.085	0.337
Number of woody and herbaceous climber species in the herb layer	N_HL_climber	-0.869	-0.495	0.024	0.743
Number of herbaceous species	N_herb_species	-0.867	0.498	0.409	0.001
Number of herb layer species (=N_recruit_species + N_HL_climber + N_herb_species)	N_HL_species	-0.978	-0.208	0.107	0.243
Proportion of rare recruit species	Prop_rare_recruits	0.060	0.998	0.113	0.235
Bray-Curtis similarity between adults and recruits	BrayCurtis_adult_recruits	-0.939	-0.344	0.028	0.725
Sørensen similarity between adults and recruits	Sorensen_adult_recruits	-0.870	-0.494	0.029	0.705
Per capita recruitment rate per plot	Per_capita_recruitment	-0.999	0.052	0.165	0.112
Proportion of recruit species new to a plot	Prop_exclusive_recruits	-0.740	-0.673	0.073	0.404

Notes: NNR denotes the Gutianshan National Nature Reserve, China. The determination coefficient r^2 shows the proportion of variance explained. P refers to the significance of the correlation between the variables in either set, (A) or (B), and the NMDS scores, based on a permutation test of $n = 999$.

standardized (i.e., z transformed) prior to analysis, resulting in a model with intercept = 0. Model fitting started with a full set of independent variables and was simplified using backward selection. Multiple regression analyses were performed with the SAS 9.1 package, Proc reg (SAS 2002).

To obtain estimates of species richness that are unaffected by individual density, rarefaction analysis was based on Hurlbert's (1971) formula, as implemented in the vegan package in R, using a fixed number of 100 individuals per plot. Rarity was assessed by ranking all species both in the group of adult trees and shrubs as well as in the group of seedlings in the order of their

abundance across all plots. Species were considered "rare" or "common" when they occurred in the lower or upper half of all ranks, respectively (rarity threshold 50%). We also tested whether the definition of rarity had an impact on the results by considering species to be "rare" when they occurred in the lower quartile (rarity threshold of 25%).

To relate the number of recruits to the number of adults, the census from the central 10 × 10 m subplot was extrapolated to the whole plot area by multiplying all counts of recruits by 9. As Wright (2002) pointed out, the species' per capita recruitment rate should not be plotted against the species' abundance, as this takes the

form of y/x vs. x . Thus, we directly regressed the number of recruits on the number of adult plants and tested for a log–log relationship after transforming both the count data of adults and recruits by $\log_{10}(x + 1)$. We then compared the observed and expected slope and identified outliers from this prediction by plotting confidence intervals using a tolerance of ± 2 SD. To test whether the recruits of a species were concentrated in the same successional stage that was preferred by conspecific adults, we calculated the ratios of number of individuals ($x + 1$) in late successional stages (4 and 5) to their number in early successional stages (1 and 2) for each species. We then compared this ratio (expressed as a log ratio) between recruits and adults. Again, we plotted confidence intervals using a tolerance of ± 2 SD to identify outliers (e.g., long-lived pioneer species that might occur in old successional stages as adults but have recruits only in young successional stages).

For each species, per capita recruitment rates were calculated by relating the number of recruits (multiplied by 9, as explained in the previous paragraph) to the number of adult trees and shrubs. This was done at three levels: at the level of each plot, across all plots of one successional stage, and for all 27 plots of the whole study. Plot-wise per capita recruitment rates were obtained by averaging the per capita recruitment rate of all species present in a plot. Using a mixed model with successional stage as fixed factor and species identity as random factor, we tested for the impact of successional stage on species-specific per capita recruitment rate (Proc mixed [SAS 2002]).

Species similarity between adults and recruits was calculated for each plot, both based on counts of individuals using Bray-Curtis similarity and on presence/absence using the Sørensen index (Sørensen 1948). In addition, we counted those species among the recruits that were not yet present in a plot among the adults (i.e., species in a plot found exclusively in the group of recruits, not among the adults).

RESULTS

The assignment of CSPs to the five different successional stages was well reflected in the age of the largest trees in the plot. Age determination of the stem cores taken from 64 tree species was possible except for three species (*Castanopsis eyrei*, *Cyclobalanopsis myrsinaefolia*, *Cyclobalanopsis stewardiana*). Across all species and across all plots diameter at breast height (dbh) was well related to tree age (Fig. 2A). Few old trees, which were retained during harvesting, occurred even in the youngest plots. This means that in every plot 1, 2, or 3 trees might be older than the time of the harvesting event. Therefore, the fifth-largest tree in a plot was chosen as being representative of the stand age. Fig. 2B shows that the age of the fifth-largest tree closely matched the assignment to successional stages, with an age (mean \pm SD) for the successional stages 1, 2, 3, 4, and 5 of 34.7 ± 11.9 yr, 43.2 ± 6.3 yr, 66.3 ± 10.9 yr,

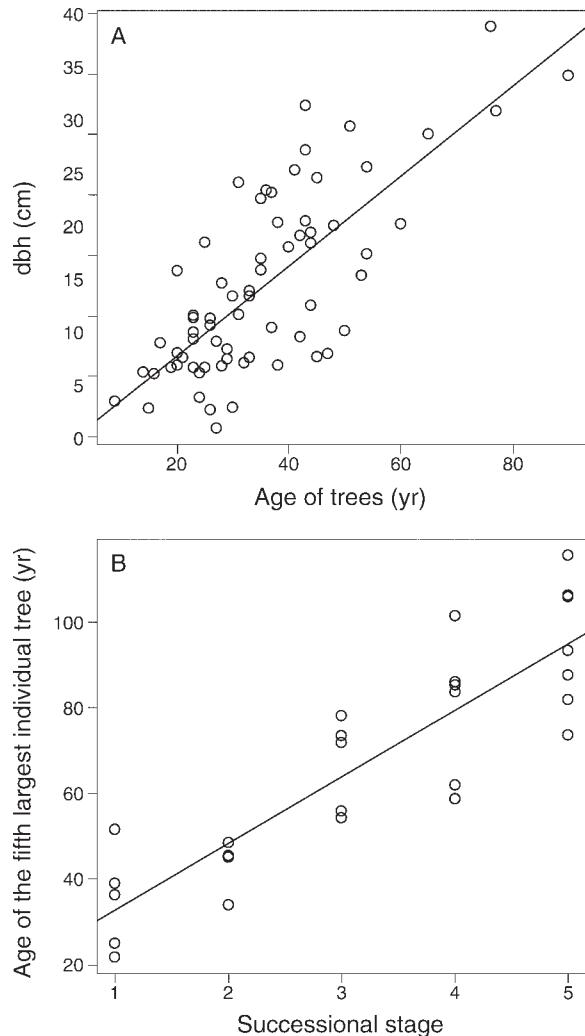


FIG. 2. Definition of plot age classes. (A) Diameter at breast height (dbh) as a function of tree age, across all comparative study plots (CSPs) and all species. The solid line shows the significant linear regression: $\text{dbh} = 4.252 + 0.371 \times \text{age}$; $r = 0.753$, $P < 0.001$. (B) Age of the fifth-largest individual tree in the plot as a function of successional stage (1, < 20 yr; 2, < 40 yr; 3, < 60 yr; 4, < 80 yr; 5, ≥ 80 yr). The solid line shows the significant linear regression: $\text{age} = 17.39 - 15.52 \times \text{successional stage}$, $r = 0.880$, $P < 0.001$.

79.4 ± 16.2 yr, and 94.8 ± 15.0 yr, respectively. The comparably high age of the successional stage 1 resulted from the fact that in some plots five or more old trees had been retained during harvesting (e.g., CSP 16, with 11 trees > 20 cm dbh).

In total, 148 woody species from 46 families were recorded with at least one individual > 1 m. A full list of species is given in the Appendix. Maximum richness was 69 woody species per 30×30 m plot. A total of 21 species occurred with only one individual in one of the CSPs, and further 14 species (but in some cases multiple individuals) occurred in only one CSP. However, these

rare species were quite evenly distributed across the successional age classes. The fidelity analysis showed that only two species were significantly concentrated in the youngest plots (*Glochidion puberum*, *Platycarya strobilacea*), and only one species significantly concentrated in the oldest plots (*Photinia glabra*) (Appendix). The community turnover rates between stages 1 and 2, 2 and 3, 3 and 4, 4 and 5 were 22%, 22%, 16%, and 11%, respectively.

The CSPs were evenly scattered and without obvious outliers in the NMDS ordination (Fig. 3). The same applied to the species. The DCA revealed a length of 3.56 standard deviation units for axis 1, showing a significant turnover of species, and thus a comparably high β diversity among CSPs. The NMDS centroids of the successional stages 1, 2, 3, 4, and 5 on axis 1 were -0.65 , -0.24 , 0.02 , 0.23 , and 0.39 , respectively, thus showing decreasing differences between successive stages with increasing stand age.

Post hoc correlation of NMDS scores with variables describing abiotic plot characteristics and stand structure (Fig. 3A), and with diversity variables of the different strata and life forms (Fig. 3B), allowed an interpretation of the gradients encountered (Table 1). NMDS axis 1 was significantly positively correlated with successional stage: plots of early successional stages are located on the left side and plots of late successional age on the right side in Fig. 3A. Along with increasing successional age, structural variables such as height of the tree and shrub layers increased from left to right in Fig. 3A, while shrub layer cover, number of herbaceous species, and number of individuals of adult trees and shrubs (>1 m height) decreased (Fig. 3B). The structural variables also showed significant univariate correlations with successional stage (Table 2). For example, density of individuals decreased with successional stage ($r = -0.772$), with a maximum and minimum density of 1233 and 207 individuals per 30×30 m plot, respectively. Using the age of the fifth-largest tree in the plot gave essentially the same significant or nonsignificant relationships for all tested variables (Table 2). Thus, in the following figures (Figs. 4, 5, and 8) the age of the fifth-largest tree is used as predictor in univariate regressions, simultaneously using different colors for the different successional stages.

The proportion of deciduous species in the group of adult shrubs and trees decreased significantly with successional stage, both in the multivariate permutation test (Table 1) and in the univariate regression (Table 2). On average, youngest stands (<20 yr) had a degree of deciduousness of 44% and 39% in terms of number of species and individuals, respectively, while the proportion for the oldest stands (≥ 80 yr) were 26% and 8%, respectively.

The NMDS ordination in Fig. 2 shows that adult species richness increased with successional stage, although this relationship was not significant according to the permutation test (Table 1) and in the univariate

regression (Table 2). Adult species richness became significant once corrected for the different number of individuals per 30×30 m plot by rarefaction to 100 individuals per plot (Fig. 4, Tables 1 and 2).

The explanatory variable "successional stage," according to which the plots had been chosen, was also among the four predictor variables that were finally retained in the optimized multiple regression model to explain species richness of adult shrubs and trees in the CSPs (Table 3). The results of this model were the same, irrespective of whether adult species richness per 30×30 m plot area (Table 3) or per 100 individuals (data not shown) was used as a dependent variable. The three other predictor variables were height, cover of the lower tree layer (T2), and amount of bare ground. Further environmental variables had little influence on adult species richness. For example, neither aspect (eastness and northness) nor slope had significant effects on tree and shrub species composition (Table 1). Elevation was significantly positively correlated with NMDS axis 2 (Fig. 3A, Table 1), but was related neither to adult species richness ($r = 0.024$, $P = 0.906$) nor to successional stage (Table 2).

The proportion of rare species both among adults (Fig. 5A) and among recruits (Fig. 5B) was not related to the age of the fifth-largest tree or to successional stage. The pattern was essentially the same when other thresholds of rarity were chosen (e.g., 25% of the least abundant species, Table 2). The regression line of the relationship between number of adult species and number of recruit species closely matched the 1:1 line, indicating a constant recruitment rate across all levels of abundance of adults (Fig. 6A). With the exception of 12 species, all others were included in the confidence intervals of ± 2 SD. Among these 12 species, eight were not found among the adults but occurred as seedlings in high numbers (*Evodia fargesii*, *Lithocarpus harlandii*, *Choerospondias axillaris*, *Ardisia punctata*, *Pertusadina hainanensis*, *Cyclocarya paliurus*, *Manglietia yuyuanensis*, and *Sapindus mukorossi*), only two species occurred each with two (*Lespedeza formosa* and *Tarenna molissima*), one species with three (*Wikstroemia monnula*) and one species with four (*Glochidion puberum*) adult individuals. With a few exceptions, all species showed the tendency to have recruits in the same successional stages in which the adults were more abundant (Fig. 6B). Species with a preferential occurrence of adults in early successional plots (marked in red in Fig. 6B) also had a higher proportion of recruits in these plots. Conversely, late successional adult species (marked in blue in Fig. 6B) also had a higher proportion of recruits in these late successional stages. There were only nine outliers, i.e., species where the preferred occurrence of recruits according to successional stage diverged from that of adults. This allows us, for example, to identify long-lived pioneers, i.e., species with a preferred recruitment in the early successional

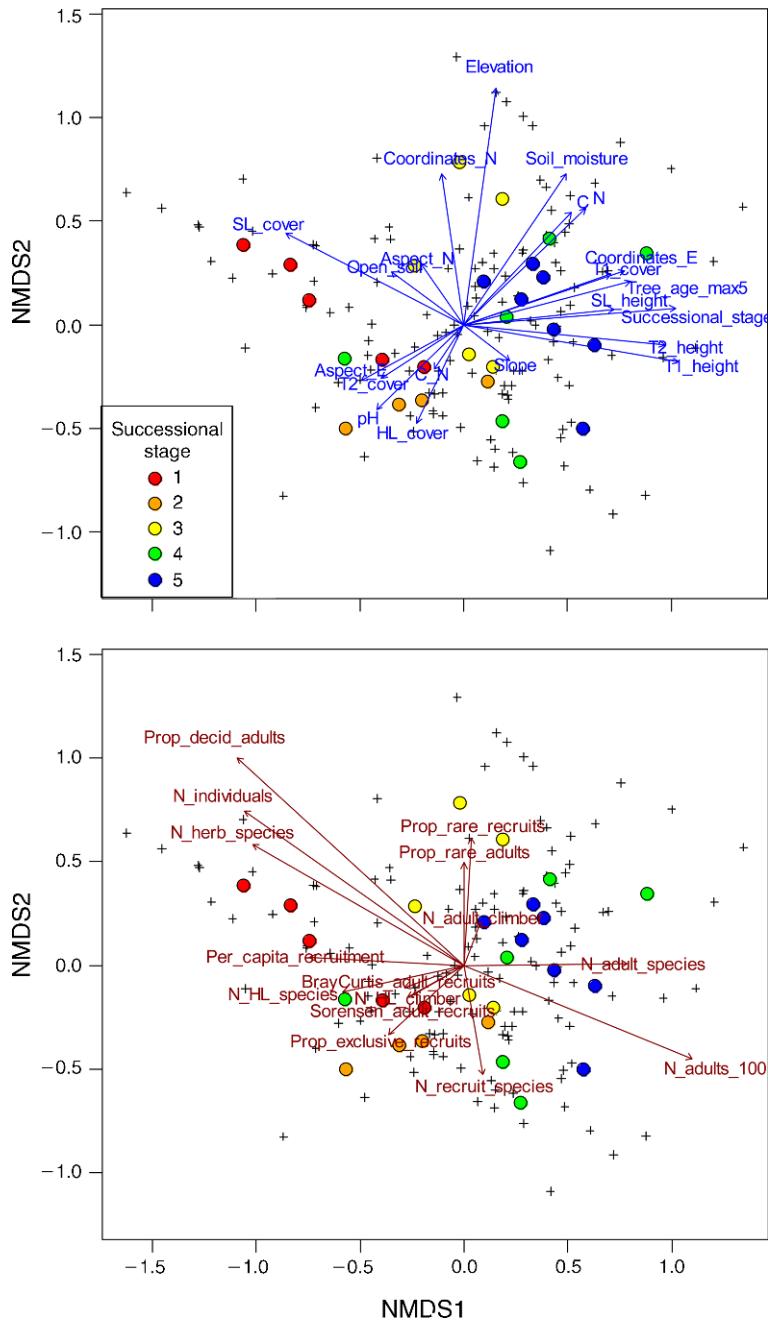


FIG. 3. Nonmetric multidimensional scaling (NMDS) ordination of abundance of all adult tree and shrub species with at least one individual >1 m in height ($n = 148$, black “plus” [+] symbols) in the Comparative Study Plots (CSP, $n = 27$); colored circles indicate the different successional stages. In various runs, a stable solution was found, on average, after four random starts (stress = 15.86). (A) Post hoc correlation of variables describing plot characteristics and structure. (B) Post hoc correlation of variables describing species diversity of the different strata and life forms. See the *Methods* section; see also Table 1 for abbreviations and significance of correlations.

stages but a preferential occurrence of adults in late successional stages (*Toxicodendron sylvestri*, *Litsea elongata*).

The plot averages of per capita recruitment rates of all adult species in a plot were not correlated with the proportion of rare species in a plot (Fig. 7). Per capita

recruitment rates were also not related to successional stage, which was revealed by a mixed model based on the species-specific per capita recruitment rates in each plot and using species as a random factor ($y = -0.131x + 10.492$, $t = -0.17$, $df = 294$, $P = 0.864$). Averaged over all plots for each successional stage, the per capita

TABLE 2. Results of univariate relationships of different response variables to successional stage (columns on the left) or to the age of the fifth-largest tree in a plot (columns on the right).

Response variables	Successional stage (stage 1-5)			Age of the fifth-largest tree [yr]		
	Slope	Correlation coefficient r	P	Slope	Correlation coefficient r	P
Density of adult trees and shrubs (number per 30 × 30 m)	-151.770	-0.772	<0.001	-7.705	-0.692	<0.001
Proportion of deciduous species in the group of adult shrubs and trees	-0.044	-0.514	0.006	-0.002	-0.506	0.007
Proportion of deciduous individuals in the group of adult shrubs and trees	-0.077	-0.556	0.003	-0.004	-0.552	0.003
Species richness of adult trees and shrubs per 30 × 30 m plot	1.978	0.282	0.154	0.097	0.311	0.222
Species richness of adult trees and shrubs per 100 individuals	2.167	0.558	0.003	0.116	0.524	0.005
Elevation (m)	33.150	0.085	0.140	1.502	0.233	0.242
Proportion of rare species among adult trees and shrubs; rarity threshold 50%	-0.005	-0.078	0.698	0.001	-0.234	0.239
Proportion of rare species among woody recruits; rarity threshold 50%	0.007	0.138	0.492	0.000	0.081	0.688
Proportion of rare species among adult trees and shrubs; rarity threshold 25%	0.000	-0.004	0.984	0.000	-0.110	0.586
Proportion of rare species among woody recruits; rarity threshold 25%	0.004	0.143	0.477	0.000	-0.053	0.794
Species richness of woody recruits	-0.143	-0.035	0.860	0.007	0.030	0.883
Similarity between species composition of adults and recruits based on counts of individuals and the Bray-Curtis index	-0.006	-0.078	0.701	0.000	-0.018	0.930
Similarity between species composition of adults and recruits based on presence/absence and the Sørensen index	-0.011	-0.219	0.272	0.000	-0.042	0.834
Number of recruit species new to a plot	-0.231	-0.080	0.692	-0.018	-0.112	0.578
Proportion of recruit species new to a plot	-0.007	-0.085	0.675	-0.001	-0.129	0.522

Notes: "Adult trees and shrubs" refers to individuals of >1 m height; "woody recruits" to seedlings ≤1 m height.

recruitment rates were 7.5, 15.4, 4.2, 8.1, and 8.5 recruits per adult for the successional stages 1, 2, 3, 4, and 5, respectively. The arithmetic mean per capita recruitment rate over all plots was 22.9 recruits per adult. In accordance with per capita recruitment rates, species richness of recruits was also not related to successional stage (Table 2).

Similarity between species composition of adults and recruits was low, with on average 0.382 and 0.556 for the Bray-Curtis and Sørensen index, respectively. In total, the 148 adult tree and shrub species (at least one individual >1 m) and the 136 recruit species (≤1 m) only had 109 species in common. In contrast to expectations, neither similarity based on counts of individuals (Fig. 8), nor on presence/absence (Table 2), showed a significant relationship to the age of the fifth-largest tree or to successional stage. However, the proportion of recruit species new to a plot (i.e., woody species with no individual >1 m in the corresponding plot) decreased with adult species richness per 30 × 30 m plot (Fig. 9), but showed no relationship to successional stage (Table 2).

DISCUSSION

Species richness increases along the successional gradient

The vegetation analysis revealed a clear successional gradient and, if corrected for a decreasing density of

individuals, an increase in species richness with time as postulated in the first hypothesis. The species turnover along the successional gradient was lower than reported in previous succession studies from temperate or tropical

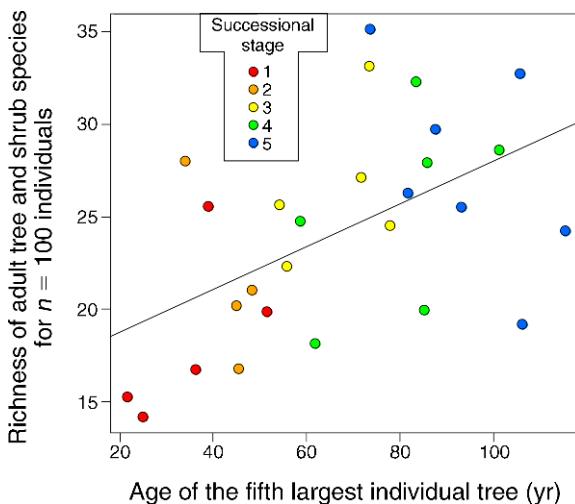


FIG. 4. Species richness based on 100 individuals (rarefaction) of adult trees and shrubs (>1 m in height) as a function of the age of the fifth largest-tree in the plot. The different colors show the successional stages (1, <20 yr; 2, <40 yr; 3, <60 yr; 4, <80 yr; 5, ≥80 yr). The solid line shows the significant linear regression: $r = 0.558$, $P = 0.003$.

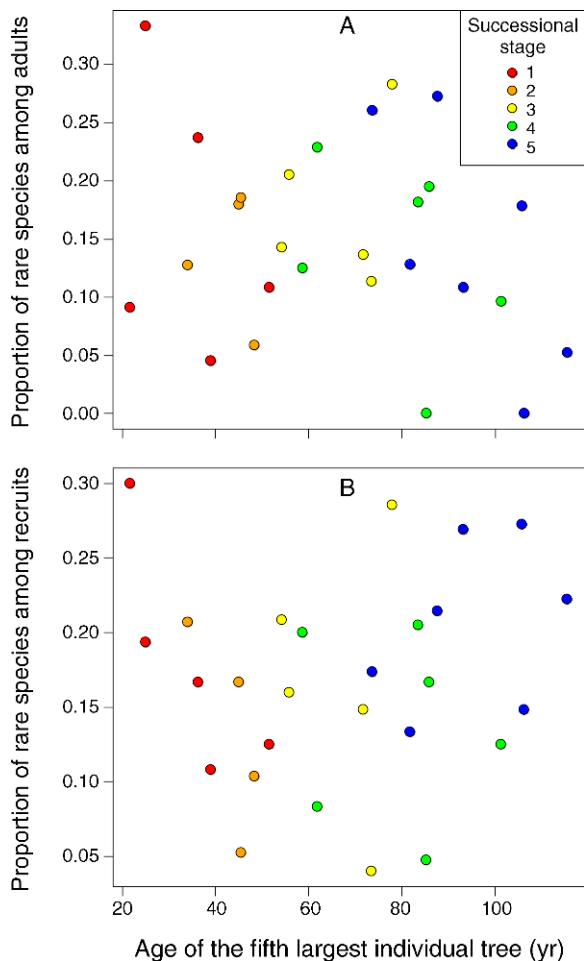


FIG. 5. Proportion of rare species calculated as the ratio of the number of rare species to the number of all species per plot as a function of the age of the fifth-largest tree in the plot. The different colors show the successional stages (1, <20 yr; 2, <40 yr; 3, <60 yr; 4, <80 yr; 5, ≥ 80 yr). (A) Proportion of rare species among adult trees and shrubs (>1 m in height): $r = -0.078$, $P = 0.689$. (B) Proportion of rare species among recruits (seedlings ≤ 1 m in height): $r = 0.158$, $P = 0.430$.

forests with a reported β diversity along the first DCA axis of ~ 5.0 (Hermy 1988, Terborgh et al. 1996). In their study of comparable forests in Zhejiang Province, Li et al. (1999) hypothesized that species composition in

subtropical forests in China is primarily driven by “initial floristic composition” (Egler 1954). Our results support the view that many woody species arrived early in succession. Similarly, the finding that there were only a few species specific to any particular successional stage lends support to the prevalence of “initial floristic composition.” This is in contrast to the general pattern of secondary succession in the wet tropics and subtropics, which is often perceived as following the concept of “relay floristics” (sensu Egler 1954, Finegan 1996, Guariguata and Ostertag 2001, Wang et al. 2006, Chazdon 2008). According to this concept, a first stage is usually dominated by herbs, shrubs, and climbers, a second stage by short-lived pioneer trees; these are replaced in a third stage by long-lived pioneers. Owing to a simultaneous continuous enrichment of shade-tolerant late-successional species, a fourth stage sometimes occurs. There are several potential reasons why the successional stages in Gutianshan were only poorly differentiated in terms of presence or absence of particular tree and shrub species. On the one hand, we might have missed the full gradient, as we deliberately excluded the early herbaceous stages directly after a clearcut. The forests may also grow much older than the oldest ones we observed at Gutianshan. On the other hand, resprouting from cut trees and shrubs might have contributed to the presence of some woody species right from the beginning of the succession (Li et al. 1999), thus rendering the initial stages similar to the older ones.

However, despite the lack of floristically distinct successional stages, the tree and shrub species in Gutianshan have not become established at once at the beginning of the succession, thus precluding a strict interpretation of the initial floristics hypothesis (Anderson 2007). In contrast to our first hypothesis, the number of species per plot did not decrease with successional stage. Rather, adult tree and shrub species richness, when expressed as number of species per 100 individuals, increased with successional stage as species accumulated with time, corresponding to the succession schemes described from the wet tropics (Finegan 1996, Kammesheidt 1998). Similar trends have been reported by Wang et al. (2007) for broad-leaved evergreen forests in Zhejiang varying in stand age from >20 yr, >43 yr, to >63 yr. With proceeding stand age, they found an

TABLE 3. Results of multiple regressions of species richness of adult trees and shrubs (>1 m height, not corrected for density of individuals) on predictor variables describing plot characteristics and structure in the comparative study plots (CSPs).

Variable	df	Parameter estimate	SE	<i>t</i>	<i>P</i>	Partial r^2
Successional_stage	1	0.701	0.334	2.10	0.047	0.161
T2_height	1	0.520	0.205	2.54	0.018	0.219
T2_cover	1	0.979	0.328	2.98	0.007	0.279
Open_soil	1	0.739	0.257	2.88	0.009	0.265

Notes: For the full list of variables and abbreviations see Table 1A. All variables were z transformed prior to analysis. Model selection was performed with backward selection eliminating independent variables according to their F statistics, until P was <0.05 for all variables. P gives the probability values for the parameter estimates. Partial r^2 is the partial variance explained using Type II sums of squares. The whole model had $df = 4$ with $df = 23$ for the error term, $F = 5.27$, $P = 0.0037$, $r^2 = 0.478$, adjusted $r^2 = 0.388$.

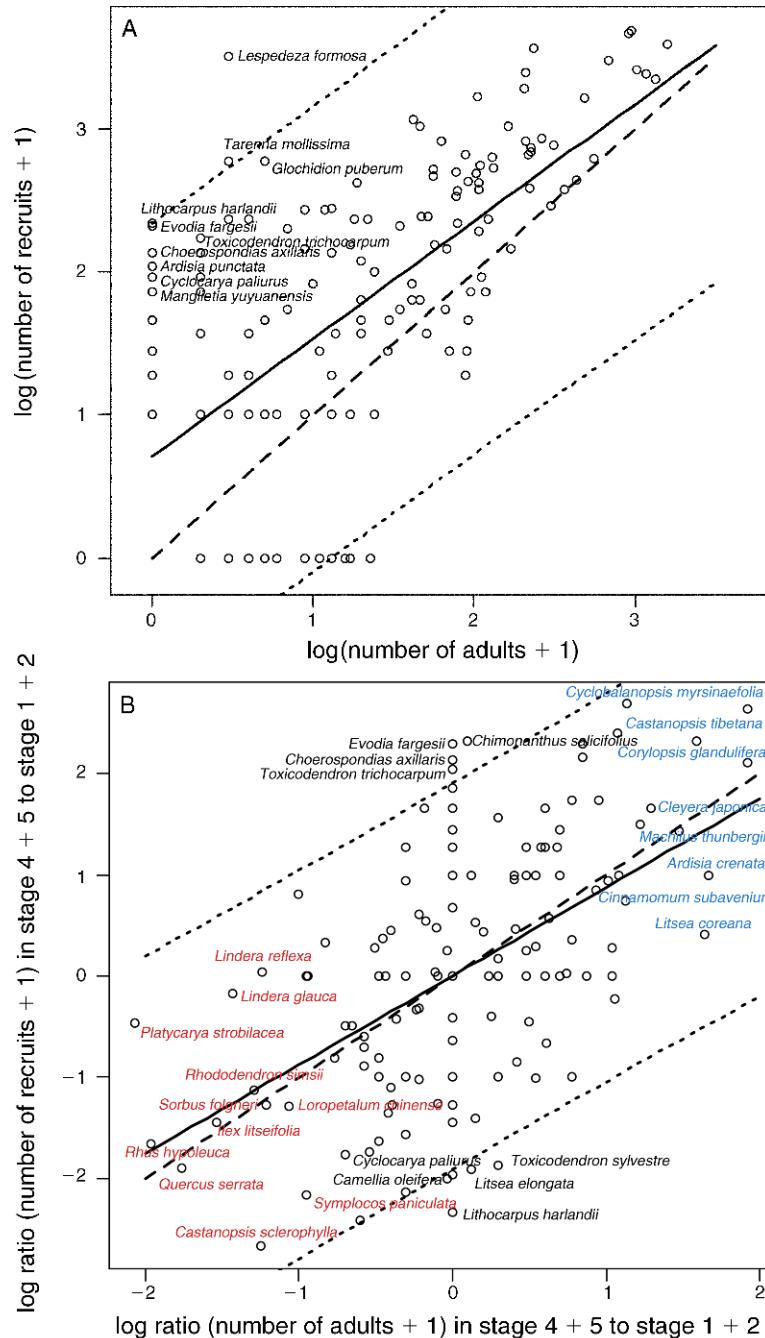


FIG. 6. (A) Number of recruits as a function of number of adults for the 175 species that occur in any of the plots as adult or recruit. Both variables were $\log_{10}(x + 1)$ -transformed. The solid regression line gives the linear regression through the origin: $y = 1.211x$, $r^2 = 0.776$, $df = 174$, $P < 0.0001$. The dashed line shows a line with slope = 1 for comparison, assuming that the per capita recruitment rate = 1 for all species. Confidence intervals are shown as dotted lines and were plotted based on a tolerance of ± 2 SD. (B) Log ratios of number of individuals in late-successional stages (4 and 5) to their number in early-successional stages (1 and 2), with log ratio of recruits regressed against log ratio of adults. Confidence intervals are shown as dotted lines and were plotted based on a tolerance of ± 2 SD. Species in the bottom left corner (some of them marked in red) are those where both adults and recruits prefer young successional stages. Species in the top right corner (some of them marked in blue) are those in which both adults and recruits prefer old successional stages. Species names in black type are outliers, with recruits concentrated in other successional stages than adult individuals (see *Results*).

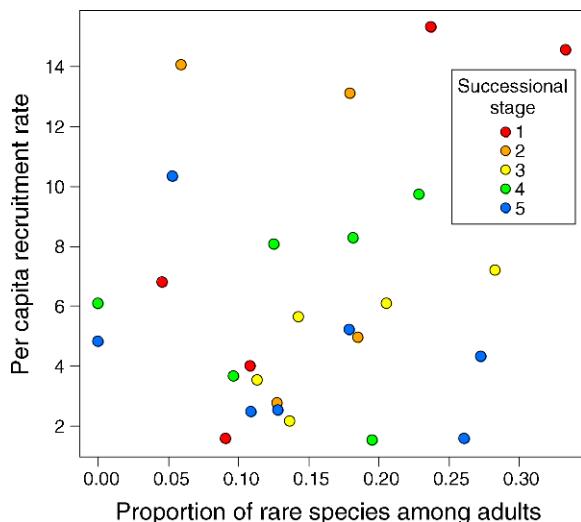


FIG. 7. Per capita recruitment rate per plot (calculated as the average of the per capita recruitment rates of each species present as adults in a plot), as a function of the proportion of rare species in a plot (calculated as the ratio of number of rare species to number of all species per plot): $r = 0.211$, $P = 0.291$. The different colors show the successional stages (1, <20 yr; 2, <40 yr; 3, <60 yr; 4, <80 yr; 5, ≥ 80 yr).

increase in richness of woody species in the shrub layer from 20 species to 38 species per 400 m² (not corrected for density of individuals). The net accumulation of species over the first 80 years of secondary succession in Gutianshan is very similar to values described from Colombia and Venezuela (Saldarriaga et al. 1996). Species number recorded on the same plot size as in our study (900 m²) increased from an average of 45 tree species (>1 cm dbh) after 12 years since the start of succession to 71 species after 80 years. Similar values have also been reported from Neotropical secondary forests (Guariguata and Ostertag 2001) or from Japan (Aiba et al. 2001). The absence of a peak in species richness at mid-successional stages, as reported from the Western Great Lakes area (Auclair and Goff 1971), may be due to the shorter time span of the successional gradient (the oldest stands at Gutianshan were not older than 180 yr), which is a typical feature of Chinese subtropical forests (e.g., Wang et al. 2006).

The increase of species richness with successional age could not be explained by the measured site characteristics. Neither soil pH nor topographical variables such as aspect and slope were related to species richness or composition of adult woody species. On the one hand, this confirms the validity of our chronosequence approach because differences in site conditions were not covarying with successional stage. On the other hand, the low level of site heterogeneity encountered for all measured variables except for elevation suggests that the sampled forests have not been predominantly shaped by abiotic conditions but by biotic processes. This finding is in contrast to single-species habitat models

developed for a subtropical permanent forest plot in Dinghushan (Guangdong Province, China), where the majority of species showed a significant dependence on slope, aspect, elevation, and convexity (Wang et al. 2009). However, data from a single plot may possibly show such effects due to spatial auto-correlation. Using data from a single 24-ha plot in Gutianshan and accounting for auto-correlation, Legendre et al. (2009) found the contribution of spatially independent habitat effects to be <5% both for explaining species richness and β diversity. They identified only 8 species out of a total of 159 species with a statistically significant indicator value for one of five distinguished habitat types (valley, mid-altitude ridges, highly convex plots, and less convex mid- and high-altitude plots). In the present study, we could not predict species occurrences from site characteristics, nor was there a strong association between species and successional stages as revealed by our fidelity analysis where only 3 out of 148 species were significantly concentrated in a particular successional stage. All these results indicate that species assembly processes at the plot level were largely random. This view is also supported by other studies from Asian subtropical broad-leaved forests, which revealed a similar “habitat generality” of most species (Aiba et al. 2001, Wang et al. 2007).

Rare species do not accumulate

Our second hypothesis of increasing proportion of rare species with successional stage was not supported. Richness of rare species among both adults and recruits was independent of the successional stage. Thus, the

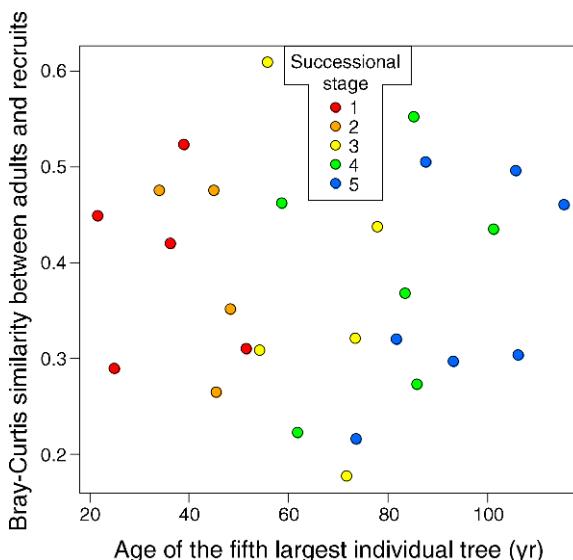


FIG. 8. Similarity between species composition of adults and recruits based on counts of individuals and the Bray-Curtis index as a function of the age of the fifth-largest tree in the plot. The different colors show the successional stages (1, <20 yr; 2, <40 yr; 3, <60 yr; 4, <80 yr; 5, ≥ 80 yr): $r = -0.078$, $P = 0.701$.

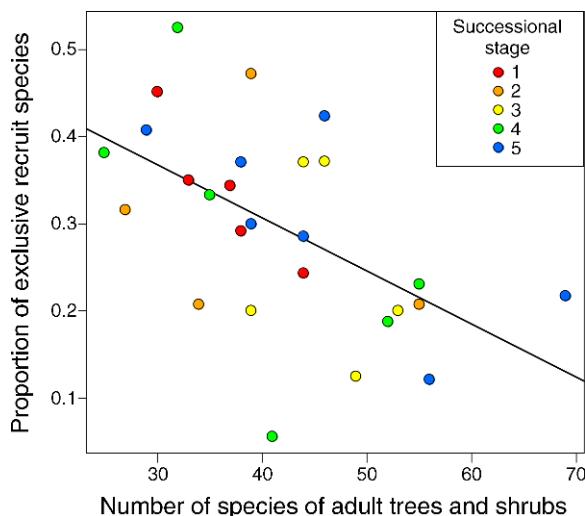


FIG. 9. Proportion of recruit species new to a plot (no individual >1 m height, i.e., exclusive recruit species) as a function of species richness of adults of trees and shrubs (>1 m height): $r = -0.549$, $P = 0.003$. The different colors show the successional stages (1, <20 yr; 2, <40 yr; 3, <60 yr; 4, <80 yr; 5, ≥ 80 yr).

increasing species richness with successional stage could not have been caused by preferential survival of rare species, thus contradicting findings from some tropical forests (Wills et al. 2006). The ratio between the density of adults and those of recruits remained remarkably constant, with the exception of only nine species; of these species, adult trees were either absent from our plots or had a very low stem density. However, rareness defined as abundance of stems in plots only captures one aspect of rarity. In Rabinowitz's (1981) system of classifying rare plants, the size of the geographical range and habitat specificity are alternative ways in which a plant can be rare. It is conceivable that the majority of woody species in our plots might be locally rare but not according to geographical range and habitat specificity, as was shown by Pitman et al. (1999) for a network of 21 forest plots in the Manu National Park (Peru). They found that most of the Amazonian forest tree species are habitat generalists, have a wide range in the South American lowlands, and attain large (i.e., >1.5 individuals/ha) population sizes at least in some localities, although their average density over the whole study area might be very low (i.e., <1 individuals/ha). Although such an analysis is still missing for Chinese subtropical forests, it seems that only a few tree species are local endemics, such as *Lithocarpus glaber* and *Machilus thunbergii* (Song 1988).

Random immigration leads to increasing species richness

Our third hypothesis, that the increasing species richness in the course of succession was caused by continuous immigration, was supported by the results.

There was a constant number of recruit species and also of exclusive recruit species, i.e., those that had not been present as adult individuals in a plot, across all successional stages. This pattern of constant arrival of new recruit species in the plot does not support the view that a large proportion of species in the early successional stages (i.e., <40 yr) originates from resprouting (Li et al. 1999, Wang et al. 2007). The constant immigration of recruit species into the plots in the course of succession and the concomitant maintenance of dissimilarity in species composition between established adults and recruits suggest effective seed dispersal into the plot from the neighborhood. The recruits did not predominantly originate from individuals growing inside the plot but to a considerable degree arrived from the outside. This implies that recruitment limitation, defined as the failure of a species to regenerate in all sites favorable for its growth and survival (Hubbell et al. 1999), occurred in both young and old successional stages, but decreased in the course of succession. The negative relationship between richness of adult woody species and the proportion of exclusive recruits indicates that the regional species pool, i.e., γ diversity of tree and shrub species, is approached more and more closely with increasing α diversity. This points to the importance of the regional species pool for preserving such species-rich subtropical forests. With a given species pool, local richness will continuously increase, even when parts of the forest are affected by occasional disturbance. Such a gradual approximation of species richness to saturation is a pattern often observed in secondary succession (Tilman 2004). Accordingly, community turnover rate, as a percentage, decreased with successional time, visible both in percentage community turnover rates based on presence/absence as well as in decreasing centroid differences between successional stages along the first NMDS axis based on species abundances. This result extends the general tendency of decelerating rates of community change with time, as described by Anderson (2007), based on presence/absence data, to data sets based on abundance. Our findings are also consistent with Hubbell's (2001) neutral theory. The virtual absence of specialist species for certain successional stages would provide some support to the community drift model (Hubbell and Foster 1986), although our floristic gradient in the course of succession precludes a fully random walk in community composition across all taxa of trees and shrubs. An exclusive random drift would also contradict the observed dominance patterns of tree species, which seem to be remarkably similar across different regions in Southeast China. Thus, there might yet be unknown species-specific differences in immigration and establishment rates, which would contradict a fully neutral model. Irrespective of absence or presence of species-specific differences, we assume that local species richness would ultimately converge toward the



PLATE 1. Chinese mixed broad-leaved forest in the Gutianshan Nature Reserve, near Hong Yuan, Zhejiang Province (CSP21). This stand is a “feng shui” forest with an estimated age of the fifth-largest tree of 106 yr (age class 5). Photo credit: H. Bruelheide.

regional species richness, or more precisely, toward the number of species drawn randomly from the regional species pool according to the density of individuals. However, in Chinese subtropical forests, high degrees of convergence between local and regional species richness may rarely occur before a new disturbance event restarts the secondary succession at a local site.

CONCLUSIONS

Local species richness and species composition in this Chinese subtropical forest appears to be mainly caused by diffuse immigration, with no dominance of particular species or dependence on particular successional stages, and with fairly constant immigration rates in the course of succession. This is consistent with results obtained from tropical permanent plots (Hubbell et al. 1999). In contrast, our current data neither support the concept of species being characteristic of certain successional stages or environmental conditions, nor the idea of differential survival of rare species. These results have important implications for the design of experimental communities, such as those that have recently been established in the biodiversity–ecosystem functioning experiment nearby (see Fig. 1C). An important lesson learned from our comparative study is the awareness that stands of young demographic age are not entirely different from old ones

with respect to species composition, richness, and other features. This means that young, experimentally established stands might yield results that can be transferred to the conditions found along natural successional gradients. Furthermore, our results suggest that it is not important to select tree species for the design of experimental communities based on rarity or environmental requirements. One of the criticisms of past biodiversity experiments was focused on the use of randomly drawn species combinations out of a constant species pool to establish a gradient of species richness (Lepš 2004). Instead, extinction scenarios based on rarity of species were advocated (Grime 2002). However, with our current knowledge, at least for subtropical forest ecosystems like the ones studied here, assembling communities randomly from the regional species pool seems to be the best strategy.

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APPENDIX

List of all adult tree and shrub species (>1 m height) encountered in the 27 comparative study plots (CSPs) of the Gutianshan National Nature Reserve (*Ecological Archives* M081-002-A1).