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Guo, D; Guo, L D; Härdtle, W; He, J S; Hector, A; Kröber, W; Kühn, P; Lang, A C;
Nadrowski, K; Pei, K; Scherer-Lorenzen, M; Shi, X; Scholten, T; Schuldt, A;
Trogisch, S; von Oheimb, G; Welk, E; Wirth, C; Wu, Y T; Yang, X; Zeng, X; Zhang,
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Community assembly during secondary forest succession in a Chinese subtropical forest

Abstract

Subtropical broad-leaved forests in southeastern China support a high diversity of woody plants. Using a comparative study design with 30330 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 10310 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.

Community assembly during secondary forest succession in a Chinese subtropical forest

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Abstract

Subtropical broad-leaved forests in south-eastern China support a high diversity of woody plants. Using a comparative study design with 30 x 30 m plots (n = 27) from five successional stages (< 20, < 40, < 60, < 80 and ≥ 80 yrs) 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 x 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 non-metric 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 amongst 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.

48

53

54 **Introduction**

55 The last decades have much improved our understanding of the forces that affect tree species

56 richness in forests. Local or community species richness, i.e. α-diversity, is increased by

57 immigration and reduced by extinction and both processes may be stochastic or deterministic

58 (MacArthur and Wilson 1967, Hubbell 2001). While stochastic immigration mainly depends

59 on the difference between regional species richness, i.e. γ-diversity, and α-diversity, and on

60 the degree of dispersal limitation (Hubbell et al. 2008), deterministic immigration additionally

61 depends on the characteristics of the immigrating species, of the receiving community and

62 interactions between the two (Rejmanek 1996, Crawley et al. 1999, Mwangi et al. 2007).

63 Stochastic extinction usually affects species with small population size (Simberloff 1988,

64 Fischer and Stöcklin 1997, Matthies et al. 2004), whereas deterministic extinction may be due

65 to environmental filtering (Lavorel and Garnier 2002) or exclusion of a plant species by

66 competitors, pathogens or herbivores (Schmid and Matthies 1994). An important mechanism

67 acting against extinction is negative density or frequency dependence, which either occurs

68 when negative interactions are less detrimental or positive interactions are more favorable

69 among different species than among individuals of the same species (Wright 2002, Wills et al.

70 2006).

71 Interestingly, not much attention has been paid to the question of how stochastic and

72 deterministic processes affect community assembly during secondary forest succession,

73 although for a number of reasons such succession series are highly suitable systems for

74 studying community assembly and diversity maintenance. First, some processes are directly

75 observable, such as recruitment and mortality (Chazdon 2008). However, other processes

76 such as the development of positive interactions are much less obvious, although it is

77 generally assumed that they increase with time, as the ecosystems get more structured and

78 more complex (Odum 1971, Margalef 1963). There is ample evidence for a temporal

79 development of complementarity from biodiversity–ecosystem functioning (BEF)

80 experiments (Tilman et al. 2001, Cardinale et al. 2007, Duffy 2009, Marquard et al. in press),

81 but not much is known from secondary forest succession series. Second, the general

82 development of species richness along successional series is well known for many forest types

83 (Howard and Lee 2003, Chazdon 2008). According to Howard and Lee (2003), four main

84 patterns can be distinguished: species richness can monotonously decrease or increase with

85 ongoing succession, peak at middle successional stages or may not show any temporal trend.

86 The absence of any trend might occur if changes in successional stages involve changes in

87 environmental conditions to which only a limited but unpredictable number of species are

88 adapted (Denslow 1980). While these patterns describe the net changes in species richness

89 during succession, they do not discuss the underlying community assembly processes, i.e.

90 immigration and extinction dynamics. So far, it has not been analyzed to which extent the

91 above mentioned negative and positive forces act on net species richness during the course of

92 secondary forest succession.

93 A continuous decrease in diversity during succession, caused by prevalence of extinction

94 processes, is consistent with the hypothesis of initial floristic composition (Egler 1954): At

95 the beginning of succession a large number of species immigrate but more and more species

96 go extinct as competition for increasingly depleted resources, mainly light, increases over

97 time. In addition, stochastic extinction increases when individuals increase in size and the

98 overall density of individuals declines. This sampling effect (Denslow 1995, Hubbell et al.

99 1999) also contributes to decreasing richness. In contrast, two major processes might promote

100 an increase in tree species richness with successional age, either resulting in a monotonous

101 increase or in a mid-successional peak:

102 First, effects of negative density and frequency dependence, for example Janzen/Connell-

103 effects (Janzen 1970, Connell 1971, Condit et al. 1992, Freckleton and Lewis 2006), might

104 accumulate with time, and thus be more prominent in mature stands. Studying the diversity in

105 subtropical and tropical forests in Queensland, Australia, Connell et al. (1984) called this

106 effect compensatory recruitment, as it would compensate for the tendency of competitively

107 stronger species to increase at the expense of weaker ones. Based on the observation that

108 more common species had fewer seedling recruits per adult than rarer species, Connell et al.

109 (1984) suggested that rare species were favored over common ones in terms of a per capita

110 recruitment rate. Recently, Wills et al. (2006) compared the diversity of cohorts of different

111 age and size in repeated census intervals of seven tropical forest plots. They found preferential

112 establishment and survival of less abundant compared to more abundant species, which

113 resulted in an increased enrichment of rare species with successional stage. As a consequence,

114 rare species would be prevented from local extinction and diversity would increase from the

115 group of seedlings to the one of young and old trees.

116 Second, young successional stages might experience continuous immigration from late

117 successional stages because those contain a considerable part of the regional species pool.

118 Thus, young successional stages might start with a low number of tree species and then

119 become enriched with time. Given a constant stream of immigrants from a random set of

120 species, newly established cohorts would be expected to have a low floristic similarity to

121 already established ones when the number of residents is low, such as in young stands. With

122 progressing succession composition of new cohorts would become increasingly similar to the

123 established species, because more and more of the newly arriving species would be already

124 present in the community (Anderson 2007). However, similarity between recruits and the

125 established trees might also reach local minima if there are clear successional stages that

126   fundamentally differ in species composition (Chao et al. 2005).

127   In this paper, we ask whether tree species richness increases or decreases with increasing age

128   of successional stages in a warm-temperate laurophyllous forest (in the following called

129   subtropical forest) in Zhejiang Province, China (see below), and how stochastic or

130   deterministic immigration and extinction may contribute to the net changes in species

131   richness. These subtropical mixed forests are of particular interest for diversity research since

132   they are similarly rich in woody species as tropical forests (Wills et al. 2006, Condit 1995,

133   Legendre et al. 2009). In addition, they represent a formerly widespread ecosystem in South

134   and East China (Wu 1980), which currently is under high pressure from intensive land use

135   (Wang et al. 2007). Our motivation to address the impact of successional age on diversity

136   originates from a recently initiated experiment that uses a large set of subtropical tree and

137   shrub species in Jiangxi, China, close to the forest plots studied here, to explore the

138   relationships between biodiversity and ecosystem functioning (www.bef-china.de). In the

139   experiment, artificial stands of defined tree species diversity levels are established by planting

140   seedlings, and in consequence, during the first years will only reflect the conditions of young

141   successional stages with respect to microclimate, food web structure and nutrient fluxes and

142   pools. Thus, we were interested to learn to which extent young forest stands differ from old

143   ones in all types of ecosystem functioning variables. This paper is the first contribution to this

144   topic, asking how much tree and shrub richness and variables related to richness vary along a

145   gradient of different stand ages. Our specific hypotheses were:

146   (1) Richness of tree and shrub species recorded on a fixed plot size is highest in young

147   successional stages and decreases in the course of succession, mainly because of declining

148   density of individuals. If the sampling effect is taken into account, i.e. if richness is corrected

149   for a decreasing density of individuals in the course of succession, richness is expected to

150   increase. In addition, we tested whether successional stage is a better predictor for species

151   richness than other variables related to structure and site characteristics.

152   (2) Rare species increasingly contribute to the potential effect of increasing richness with

153   successional age. A preferential survival of rare species provided, an increase in proportions

154   of rare species should be less conspicuous in seedlings as compared to adult trees and shrubs.

155   Consequently, a higher contribution of rare species should also be visible in a higher per

156   capita recruitment success of rare species as compared to common ones as well as higher

157   average per capita recruitment rates of plots containing a higher proportion of rare species.

158   (3) In contrast to the former hypotheses, which are based on the assumption of a differential

159   recruitment of common and rare species, we further hypothesized that establishment from a

160   common recruitment pool could be a random process. Assuming continuous but random

161   immigration, the richness of recruits should be constant over the different successional stages.

162   However, given a limited regional species pool and increasing richness with successional

163   time, the probability that species new to a plot would be among the recruits, i.e. those that are

164   not yet present as adult individuals, should decrease in the course of succession. Likewise, the

165   similarity in species composition between established adults and recruits is expected to

166   decrease.

167

168   **Materials and Methods**

169   *Study site*

170   The Gutianshan National Nature Reserve (NNR) is located in the western part of Zhejiang

171   Province (29º8'18"–29º17'29" N, 118º2'14"–118º11'12" E, Fig. 1). The forest is representative

172   of Chinese mixed broad-leaved forests (Wu 1980, Hu and Yu 2008, Legendre et al. 2009),

173   with evergreen species dominating the forest in number of individuals (Yu et al. 2001) but

174   with approximately similar proportions of deciduous species in terms of species number (Lou

175   and Jin 2000). A total of 1426 seed-plant species of 648 genera and 149 families has been

176   recorded as occurring naturally in the NNR. About 258 of the species are woody (Lou and Jin

177   2000). The Gutianshan NNR has an area of approximately 81 km^2, was initially established as

178 a National Forest Reserve in 1975 and became a National Nature Reserve in 2001. The NNR

179 comprises a large portion of broad-leaved forests of advanced successional stages (Hu & Yu

180 2008), which have not been managed since the beginning of the 1990s, as well as young

181 successional stages and conifer plantations, mainly of the economically important timber

182 species *Cunninghamia lanceolata* and *Pinus massoniana* (for author names of species see

183 Appendix 1).

184 Most of the stands are secondary forests, evidenced by maximum tree ages of only 180 years,

185 by the presence of relicts of agricultural terraces in almost all plots and by the presence of

186 charcoal in almost all soil profiles. Within and adjacent to the Gutianshan NNR extensive

187 deforestation has occurred during the Great Leap Forward in the 1950s, as in most parts of

188 Southeast China. However, owing to very steep slopes with some of them exceeding 30°, the

189 Gutianshan area was only marginally usable for agricultural activities, and thus an

190 exceptionally intact forest cover has been preserved.

191 The climate at Gutianshan NNR is warm-temperate with a short dry season in November and

192 December and with warm summers. The climate conditions are characteristic of the

193 subtropics with an annual average temperature of 15.1 °C, January minimum temperatures of

194 −6.8 °C, July maximum temperatures of 38.1 °C and an accumulated temperature sum (≥ 5

195 °C) of 5221.5 degree days per year.

196 *Study design*

197 Plots were randomly selected, stratified by successional age. In the following the plots are

198 called Comparative Study Plots (CSPs). Different successional ages are the result of

199 differences in elapsed time since the last forest harvesting, carried out manually by the local

200 population for timber and fire-wood. Five successional stages were distinguished according to

201 the age of the oldest tree individuals in a plot, supported by additional knowledge of the last

202 logging event in this part of the forest and local status as 'feng shui' forest (1: < 20 yrs, 2: <

203 40 yrs, 3: < 60 yrs, 4: < 80 yrs, 5: $\geq$ 80 yrs). 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 CPSs. CSP locations within strata were selected randomly; however, due to inaccessibility and extremely steep slopes (> 50°), 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 yrs), 4 (< 40 yrs), 5 (< 60 yrs), 6 (< 80 yrs) and 7 (≥ 80 yrs).

Species recording was performed between May and October 2008 with several visits per plot. Each CSP has a size of 30 x 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 (< 2mm) 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 elementar analyzer. Since all soil samples are non-calcareous, 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, in the following called recruits) were recorded in a central subplot of 10 x 10 m on the ground. All individuals were

230 identified to the species level, making use of herbarium samples and comparisons with

231 correctly identified individuals, and counted per species. The proportion of unidentifiable

232 individuals (> 1 m height) in a CSP ranged between 0–2.3 %. These individuals were not

233 included in the subsequent data analysis. All measures in this paper are expressed per area on

234 the ground (i.e. not converted to horizontal projection area).

235

236 *Data analysis*

237 We calculated the concentration of all species in one of the five successional stages, using the

238 Phi value as measure of fidelity, calculated with the Juice software (Chytrý et al. 2002). The

239 Phi values were tested for significance by Fisher's exact test, using a significance level of

240 p=0.01. At this level a species would be identified as being significantly characteristic of a

241 successional stage if, for example, it occurred at least in 3 plots of this stage (assuming that

242 the stage comprised 4 to 7 plots), but not in the other successional stages. The presence and

243 absence of species in the different successional stages was used to calculate community

244 turnover rates between successional stages according to Anderson (2007), defined as number

245 of species that were either new to a successional stage or had disappeared, divided by the total

246 sum of species in the preceding and subsequent successional stage. To analyze the floristic

247 composition of all woody species we employed non-metric multidimensional scaling (NMDS)

248 using counts of individuals per CSP and Bray-Curtis dissimilarity. The statistics were

249 computed with R (R Development Core Team 2008), using the vegan package (Oksanen et al.

250 2006). All 148 species of trees and shrubs with at least one individual > 1 m in height were

251 used in the analysis. Wisconsin double standardization, where species are first standardized

252 by species maxima and then sites are standardized by site totals, was applied to square root

253 transformed abundance data. Default options were used for scaling, so that one unit means

254 halving of community similarity from replicate similarity. Species scores were added as

255 weighted averages. In a subsequent multiple regression, the NMDS plot scores on axes 1 and

256 2 were related to (i) variables describing plot characteristics (elevation, aspect, slope,

257 geographical coordinates, height and cover of the different layers, coverage of bare ground,

258 soil moisture, pH, C, N and C/N ratio) and successional stage and (ii) to variables related to

259 species richness (number of woody species and woody lianas [height > 1 m] in the 30 x 30 m

260 plot as well as number of herb species, woody recruit species [seedlings], woody climber

261 species and herb climber species in the 10 x 10 m subplot [only recorded if height ≤ 1 m]).

262 The significance of the correlations was assessed using permutation tests (n=999). In addition,

263 a detrended correspondence analysis (DCA) was performed to determine the gradient lengths

264 and to yield an estimate of β-diversity (Jongman et al. 1995).

265 All ordinary linear regressions with single predictors were calculated with R. A multiple

266 regression was used to test the dependence of species richness of adult trees and shrubs

267 (individuals > 1 m height) on all variables describing plot characteristics and structure (for a

268 list of variables see Table 1A). The input variables were standardized (i.e. z transformed)

269 prior to analysis, resulting in a model with intercept = 0. Model fitting started with a full set of

270 independent variables and was simplified using backward selection. Multiple regression

271 analyses were performed with the SAS 9.1 package (proc reg, SAS Institute 2002, Cary,

272 North Carolina, USA).

273 To obtain estimates of species richness that are unaffected by individual density, rarefaction

274 analysis was based on Hurlbert's (1971) formula, as implemented in the vegan package in R,

275 using a fixed number of 100 individuals per plot. Rarity was assessed by ranking all species

276 both in the group of adult trees and shrubs as well as in the group of seedlings in the order of

277 their abundance across all plots. Species were considered "rare" or "common" when they

278 occurred in the lower or upper half of all ranks, respectively (rarity threshold 50%). We also

279 tested whether the definition of rarity had an impact on the results by considering species to

280 be "rare" when they occurred in the lower quartile (rarity threshold of 25%).

281 To relate the number of recruits to the number of adults, the census from the central 10 x 10 m

282   subplot was extrapolated to the whole plot area by multiplying all counts of recruits by 9. As

283   Wright (2002) pointed out, the species' per capita recruitment rate should not be plotted

284   against the species' abundance, as this takes the form of y/x versus x. Thus, we directly

285   regressed the number of recruits on the number of adult plants and tested for a log–log

286   relationship after transforming both the count data of adults and recruits by $\log_{10}(x+1)$. We

287   then compared the observed and expected slope and identified outliers from this prediction by

288   plotting confidence intervals using a tolerance of ± two standard deviations. To test whether

289   the recruits of a species were concentrated in the same successional stage that was preferred

290   by conspecific adults, we calculated the ratios of number of individuals (x+1) in late

291   successional stages (4 and 5) to their number in early successional stages (1 and 2) for each

292   species. We then compared this ratio (expressed as log ratio) between recruits and adults.

293   Again, we plotted confidence intervals using a tolerance of ± 2 standard deviations to identify

294   outliers (e.g. long-lived pioneer species that might occur in old successional stages as adults

295   but have recruits only in young successional stages).

296   For each species, per capita recruitment rates were calculated by relating the number of

297   recruits (multiplied with 9 as explained above) to the number of adult trees and shrubs. This

298   was done at three levels, at the level of each plot, across all plots of one successional stage

299   and for all 27 plots of the whole study. Plot-wise per capita recruitment rates were obtained by

300   averaging the per capita recruitment rate of all species present in a plot. Using a mixed model

301   with successional stage as fixed factor and species identity as random factor, we tested for the

302   impact of successional stage on species-specific per capita recruitment rate (proc mixed, SAS

303   9.2).

304   Species similarity between adults and recruits was calculated for each plot, both based on

305   counts of individuals using Bray-Curtis similarity and on presence/absence using the Sørensen

306   index (Sørensen 1948). In addition, we counted those species among the recruits that were not

307   yet present in a plot among the adults (i.e. species in a plot exclusively found in the group of

308 recruits, not among the adults).

309

310 **Results**

311 The assignment of CSPs to the five different successional stages was well reflected in the age

312 of the largest trees in the plot. Age determination of the stem cores taken from 64 tree species

313 was possible excep for three species (*Castanopsis eyrei, Cyclobalanopsis myrsinaefolia,*

314 *Cyclobalanopsis stewardiana*). Across all species and across all plots diameter at breast

315 height (dbh) was well related to tree age (Fig. 2A). Few old trees, which were retained during

316 harvesting, occurred even in the youngest plots. This means that in every plot 1, 2 or 3 trees

317 might be older than the time of the harvesting event. Therefore, the fifth largest tree in a plot

318 was chosen as being representative for the stand age. Fig. 2B shows that the age of the fifth

319 but largest tree closely matched the assignment to successional stages, with a mean age ($\pm$

320 standard deviation) for the successional stages 1, 2, 3, 4 and 5 of 34.7 ($\pm$ 11.9), 43.2($\pm$ 6.3),

321 66.3($\pm$ 10.9), 79.4 ($\pm$ 16.2) and 94.8 ($\pm$ 15.0) years, respectively. The comparably high age of

322 the successional stage 1 resulted from the fact that in some plots 5 or more old trees had been

323 retained during harvesting (e.g. CSP 16, with 11 trees > 20 cm dbh).

324 In total, 148 woody species from 46 families were recorded with at least one individual > 1 m.

325 A full list of species is given in Appendix 1. Maximum richness was 69 woody species per 30

326 x 30 m plot. A total of 21 species occurred only with one individual in one of the CSPs and

327 further 14 species occurred only in one CSP. However, these rare species were quite evenly

328 distributed across the successional age classes. The fidelity analysis showed that only two

329 species were significantly concentrated in the youngest plots (*Glochidion puberum,*

330 *Platycarya strobilacea*) and only one species significantly concentrated in the oldest plots

331 (*Photinia glabra*) (Appendix 1). Percent community turnover rates between stages 1 and 2, 2

332 and 3, 3 and 4, 4 and 5 were 22%, 22%, 16%, and 11%, respectively.

333 The CSPs were evenly scattered and without obvious outliers in the NMDS ordination (Fig.

334 3). The same applied to the species. The DCA revealed a length of 3.56 standard deviation

335 units for axis 1, showing a significant turnover of species, and thus a comparably high β

336 diversity among CSPs. The NMDS centroids of the successional stages 1, 2, 3, 4 and 5 on axis

337 1 were –0.65, –0.24, 0.02, 0.23 and 0.39, respectively, thus showing decreasing differences

338 between successive stages with increasing stand age.

339 Post-hoc correlation of NMDS scores with variables describing abiotic plot characteristics and

340 stand structure (Fig. 3A) and with diversity variables of the different strata and life forms

341 (Fig. 3B) allowed an interpretation of the encountered gradients (Table 1). NMDS axis 1 was

342 significantly positively correlated with successional stage: plots of early successional stages

343 are located on the left hand and plots of late successional age on the right hand in Fig. 3A.

344 Along with increasing successional age, structural variables such as height of the tree and

345 shrub layers increased from the left to the right in Fig. 3A, while shrub layer cover, number of

346 herbaceous species and number of individuals of adult trees and shrubs (> 1 m height)

347 decreased (Fig. 3B). The structural variables also showed significant univariate correlations

348 with successional stage (Table 2). For example, density of individuals decreased with

349 successional stage (r = –0.772), with a maximum and minimum density of 1233 and 207

350 individuals per 30 x 30 m plot, respectively. Using the age of the fifth largest tree in the plot

351 gave essentially the same significant or non-significant relationships for all tested variables

352 (Table 2).

353 The proportion of deciduous species in the group of adult shrubs and trees decreased

354 significantly with successional stage, both in the multivariate permutation test (Table 1) and

355 in the univariate regression (Table 2). On average, youngest stands (< 20 yrs) had a degree of

356 deciduousness of 44 % and 39 % in terms of number of species and individuals, respectively,

357 while the proportion for oldest stands (≥ 80 yrs) were 26 % and 8 %, respectively.

358 The NMDS ordination in Fig. 2 shows that adult species richness increased with successional

359 stage, although this relationship was not significant according to the permutation test (Table

360   1) and in the univariate regression (Table 2). Adult species richness became significant once

361   corrected for the different number of individuals per 30 x 30 m plot by rarefaction to 100

362   individuals per plot (Fig. 4, Table 1, 2).

363   The explanatory variable "successional stage", according to which the plots had been chosen,

364   was also among those four predictor variables that were finally retained in the optimized

365   multiple regression model to explain species richness of adult shrubs and trees in the CSPs

366   (Table 3). The results of this model were the same, irrespective of whether adult species

367   richness per 30 x 30 m plot area (Table 3) or per 100 individuals (data not shown) was used as

368   dependent variable. The three other predictor variables were height, cover of the lower tree

369   layer (T2) and amount of bare ground. Further environmental variables had little influence on

370   adult species richness. For example, neither aspect (eastness and northness) nor slope had

371   significant effects on tree and shrub species composition (Table 1). Elevation was

372   significantly positively correlated with NMDS axis 2 (Fig. 3A, Table 1), but was neither

373   related to adult species richness ($r = 0.024$, $p = 0.906$) nor to successional stage (Table 2).

374   The proportion of rare species both among adults (Fig. 5A) and among recruits (Fig. 5B) was

375   not related to the successional stage. The pattern was essentially the same when other

376   thresholds of rarity were chosen (e.g. 25% of the least abundant species, Table 2). The

377   regression line of the relationship between number of adult species and number of recruit

378   species closely matched the 1:1 line, indicating a constant recruitment rate across all levels of

379   abundance of adults (Fig. 6A). With the exception of twelve species, all were included in the

380   confidence intervals of ± two standard deviations. Among these twelve species, eight were not

381   found among the adults but occurred as seedlings in high amounts (*Evodia fargesii,*

382   *Lithocarpus harlandii, Choerospondias axillaris, Ardisia punctata, Pertusadina hainanensis,*

383   *Cyclocarya paliurus, Manglietia yuyuanensis* and *Sapindus mukorossi*), only two species

384   occurred each with two (*Lespedezea formosa* and *Tarenna molissima*), one species with three

385   (*Wikstroemia monnula*) and one species with four (*Glochidion puberum*) adult individuals.

386   With a few exceptions, all species showed the tendency to have recruits in the same

387   successional stages in which the adults were more abundant (Fig. 6B). Species with a

388   preferential occurrence of adults in early successional plots (marked in red in Fig. 6B) also

389   had a higher proportion of recruits in these plots. Conversely, late successional adult species

390   (marked in blue in Fig. 6B) also had a higher proportion of recruits in these late successional

391   stages. There were only nine outliers, i.e. species of which the preferred occurrence of recruits

392   according to successional stage diverged from that of adults. This allows, for example, to

393   identify long-lived pioneers, i.e. species with a preferred recruitment in the early successional

394   stages but a preferential occurrence of adults in late successional stages (*Toxicodendron*

395   *sylvestre, Litsea elongata).*

396   The plot averages of per capita recruitment rates of all adult species in a plot were not

397   correlated with the proportion of rare species in a plot (Fig. 7). Per capita recruitment rates

398   were also not related to successional stage, which was revealed by a mixed model based on

399   the species-specific per capita recruitment rates in each plot and using species as random

400   factor (y = –0.131 x + 10.492, t = –0.17, df = 294, p = 0.864). Averaged over all plots for each

401   successional stage, the per capita recruitment rates were 7.5, 15.4, 4.2, 8.1 and 8.5 recruits per

402   adult for the successional stages 1, 2, 3, 4 and 5, respectively. The arithmetic mean per capita

403   recruitment rate over all plots was 22.9 recruits per adult. In accordance with per capita

404   recruitment rates, species richness of recruits was also not related to successional stage (Table

405   2).

406   Similarity between species composition of adults and recruits was low, with on average 0.382

407   and 0.556 for the Bray-Curtis and Sørensen index, respectively. In total, the 148 adult tree and

408   shrub species (at least one individual > 1 m) and the 136 recruit species (≤ 1 m) only had 109

409   species in common. In contrast to expectations, neither similarity based on counts of

410   individuals (Fig. 8), nor on presence/absence (Table 2) showed a significant relationship to

411   successional stage. However, the proportion of recruit species new to a plot (i.e. woody

412 species with no individual > 1 m in the corresponding plot) decreased with adult species

413 richness per 30 x 30 m (Fig. 9), but showed no relationship to successional stage (Table 2).

414

415 **Discussion**

416 *Species richness increases along the successional gradient*

417 The vegetation analysis revealed a clear successional gradient and, if corrected for a

418 decreasing density of individuals, an increase in species richness with time as postulated in

419 the first hypothesis. The species turnover along the successional gradient was lower than

420 reported in previous succession studies from temperate or tropical forests with a reported β-

421 diversity along the first DCA axis of about 5.0 (Hermy 1988, Terborgh et al. 1996). In their

422 study of comparable forests in Zhejiang Province, Li et al. (1999) hypothesized that species

423 composition in subtropical forests in China is primarily driven by 'initial floristic

424 composition' (Egler 1954). Our results support the view that many woody species arrived

425 early in succession. Similarly, the finding that there were only very few species specific to

426 any particular successional stage lends support to the prevalence of 'initial floristic

427 composition'. This is in contrast to the general pattern of secondary succession in the wet

428 tropics and subtropics, which is often perceived as following the concept of 'relay floristics'

429 (*sensu* Egler 1954; Finegan 1996, Guariguata and Ostertag 2001, Wang et al. 2006, Chazdon

430 2008). According to this concept, a first stage is usually dominated by herbs, shrubs and

431 climbers, a second stage by short-lived pioneer trees; these are replaced in a third stage by

432 long-lived pioneers. Owing to a simultaneous continuous enrichment of shade-tolerant late-

433 successional species, sometimes a fourth stage occurs. There are several potential reasons

434 why the successional stages in Gutianshan were only poorly differentiated in terms of

435 presence or absence of particular tree and shrub species. On the one hand, we might have

436 missed the full gradient as we deliberately excluded the early herbaceous stages directly after

437 a clear cut. The forests may also grow much older than the oldest ones we observed at

438   Gutianshan. On the other hand, resprouting from cut trees and shrubs might have contributed

439   to the presence of some woody species right from the beginning of the succession (Li et al.

440   1999), thus rendering the initial stages similar to the older ones.

441   However, despite the lack of floristically distinct successional stages, the tree and shrub

442   species in Gutianshan have not become established at once at the beginning of the succession,

443   thus precluding a strict interpretation of the initial floristics hypothesis (Anderson 2007). In

444   contrast to our first hypothesis, the number of species per plot did not decrease with

445   successional stage. Rather, adult tree and shrub species richness, when expressed as number

446   of species per 100 individuals, increased with successional stage as species accumulated with

447   time, corresponding to the succession schemes described from the wet tropics (Finegan 1996,

448   Kammesheidt 1998). Similar trends have been reported by Wang et al. (2007) for broad-

449   leaved evergreen forests in Zhejiang varying in stand age from > 20 yrs, >43 yrs, > 63 yrs to $\geq$

450   63 years. With proceeding stand age, they found an increase in richness of woody species in

451   the shrub layer from 20 species to 38 species per 400 m^2 (not corrected for density of

452   individuals). The net accumulation of species over the first 80 years of secondary succession

453   in Gutianshan is very similar to values described from Colombia and Venezuela (Saldarriaga

454   et al. 1996). Species number recorded on the same plot size as in our study (900 m^2) increased

455   from on average 45 tree species (> 1 cm dbh) after 12 years since start of succession to 71

456   species after 80 years. Similar values have also been reported from neotropical secondary

457   forests (Guariguata and Ostertag 2001) or from Japan (Aiba et al. 2001). The absence of a

458   peak in species richness at mid-successional stages, as reported from the Western Great Lakes

459   area (Auclair and Goff 1971) may be due to the shorter time span of the successional gradient

460   (the oldest stands at Gutianshan were not older than 180 yrs), which is a typical feature of

461   Chinese subtropical forests (e.g. Wang et al. 2006).

462   The increase of species richness with successional age could not be explained by the

463   measured site characteristics. Neither soil pH nor topographical variables such as aspect and

464 slope were related to species richness or composition of adult woody species. On the one

465 hand, this confirms the valididy of our chronosequence approach because differences in site

466 conditions were not covarying with successional stage. On the other hand, the low level of site

467 heterogeneity encountered for all measured variables except for elevation suggests that the

468 sampled forests have not been predominantly shaped by abiotic conditions but by biotic

469 processes. This finding is in contrast to single-species habitat models developed for a

470 subtropical permanent forest plot in Dinghushan (Guangdong Province, China), where the

471 majority of species showed a significant dependence on slope, aspect, elevation and convexity

472 (Wang et al. 2009). However, data from a single plot may possibly show such effects due to

473 spatial auto-correlation. Using data from a single 24 ha plot in Gutianshan and accounting for

474 auto-correlation, Legendre et al. (2009) found the contribution of spatially-independent

475 habitat effects to be less than 5% both for explaining species richness and β-diversity. They

476 identified only eight species out of a total of 159 species with a statistically significant

477 indicator value for one of five distinguished habitat types (valley, mid-altitude ridges, highly

478 convex plots, and less convex mid- and high-altitude plots). In the present study, we could

479 neither predict species occurrences from site characteristics, nor was there a strong association

480 between species and successional stages as revealed by our fidelity analysis where only three

481 out of 148 species were significantly concentrated in a particular successional stage. All these

482 results indicate that species assembly processes at the plot level were largely random. This

483 view is also supported by other studies from Asian subtropical broad-leaved forests, which

484 revealed a similar "habitat generality" of most species (Aiba et al. 2001, Wang et al. 2007).

485

486 *Rare species do not accumulate*

487 Our second hypothesis of increasing proportion of rare species with successional stage was

488 not supported. Richness of rare species amongst both adults and recruits was independent of

489 the successional stage. Thus, the increasing species richness with successional stage could not

490   have been caused by preferential survival of rare species, thus contradicting findings from

491   some tropical forests (Wills et al. 2006). The ratio between the density of adults and those of

492   recruits remained remarkably constant with the exception of only nine species, of which adult

493   trees were either absent from our plots or had a very low stem density. However, rareness

494   defined as abundance of stems in plots only captures one aspect of rarity. In Rabinowitz's

495   (1981) system of classifying rare plants, the size of the geographical range and habitat-

496   specificity are alternative ways in which a plant can be rare. It is conceivable that the majority

497   of woody species in our plots might be locally rare but not according to geographical range

498   and habitat-specificity, as was shown by Pitman et al. (1999) for a network of 21 forest plots

499   in the Manu National Park (Peru). They found that most of the Amazonian forest tree species

500   are habitat generalists, have a wide range in the South American lowlands and attain large

501   (i.e. > 1.5 individuals ha^{-1}) population sizes at least in some localities, although their average

502   density over the whole study area might be very low (i.e. < 1 individuals ha^{-1}). Although such

503   an analysis is still missing for Chinese subtropical forests, it seems that only a few tree species

504   are local endemics, such as *Lithocarpus glaber* and *Machilus thunbergii* (Song 1988).

505

Random immigration leads to increasing species richness

507   Our third hypothesis that the increasing species richness in the course of succession was

508   caused by continuous immigration was supported by the results. There was a constant number

509   of recruit species and also of exclusive recruit species, i.e. those that had not been present as

510   adult individuals in a plot, across all successional stages. This pattern of constant arrival of

511   new recruit species in the plot does not support the view that a large portion of species in the

512   early successional stages (i.e. < 40 yrs) originates from resprouting (Li et al. 1999, Wang et al.

513   2007). The constant immigration of recruit species into the plots in the course of succession

514   and the concomitant maintenance of dissimilarity in species composition between established

515   adults and recruits suggest effective seed dispersal into the plot from the neigborhood. The

516 recruits did not predominantly originate from individuals growing inside the plot but to a

517 considerable degree arrived from the outside. This implies that recruitment limitation, defined

518 as the failure of a species to regenerate in all sites favorable for its growth and survival

519 (Hubbell et al. 1999), occurred in both young and old successional stages, but decreased in the

520 course of succession. The negative relationship between richness of adult woody species and

521 the proportion of exclusive recruits indicates that the regional species pool, i.e. γ diversity of

522 tree and shrub species is more and more approached with increasing α diversity. This points

523 to the importance of the regional species pool for preserving such species-rich subtropical

524 forests. With a given species pool, local richness will continuously increase, even when parts

525 of the forest are affected by occasional disturbance. Such a gradual approximation of species

526 richness to saturation is a pattern often observed in secondary succession (Tilman 2004).

527 Accordingly, the percent community turnover rate decreased with successional time, both

528 visible in percent community turnover rates based on presence/absence as well as in

529 decreasing centroid differences between successional stages along the first NMDS axis based

530 on species abundances. This result extends the general tendency of decelerating rates of

531 community change with time, as described by Anderson (2007) based on presence/absence

532 data, to datasets based on abundance. Our findings are also consistent with Hubbell's (2001)

533 neutral theory. The virtual absence of specialist species for certain successional stages would

534 provide some support to the community drift model (Hubbell et al. 1986), although our

535 floristic gradient in the course of succession precludes a fully random walk in community

536 composition across all taxa of trees and shrubs. An exclusive random drift would also

537 contradict the observed dominance patterns of tree species, which seem to be remarkably

538 similar across different regions in Southeast China. Thus, there might be yet unknown

539 species-specific differences in immigration and establishment rates, which would contradict a

540 fully neutral model. Irrespective of absence or presence of species-specific differences we

541 would assume that local species richness would ultimately converge towards the regional

542 species richness, or more precisely, towards the number of species drawn randomly from the

543 regional species pool according to the density of individuals. However, in Chinese subtropical

544 forests high degrees of convergence between local and regional species richness may rarely

545 occur before a new disturbance event restarts the secondary succession at a local site.

546

547 **Conclusions**

548 Local species richness and species composition in this Chinese subtropical forest appears to

549 be mainly caused by unspecific immigration, with fairly constant immigration rates in the

550 course of succession. This is consistent with results obtained from tropical permanent plots

551 (Hubbell et al. 1999). In contrast, our current data neither support the concept of species being

552 characteristic of certain successional stages or environmental conditions, nor the idea of

553 differential survival of rare species. These results have important implications for the design

554 of experimental communities, as those that have been recently established in the biodiversity–

555 ecosystem functioning experiment nearby (see Fig. 1C). An important lesson learned from our

556 comparative study is the awareness that stands of young demographic age are not entirely

557 different from old ones with respect to species composition, richness and other features. This

558 means that young experimentally established stands might yield results that can be transferred

559 to the conditions found along natural successional gradients. Furthermore, our results suggest

560 that it is not important to select tree species for the design of experimental communities based

561 on rarity or environmental requirements. One of the criticisms of past biodiversity

562 experiments focused on the use of randomly drawn species combinations out of a constant

563 species pool to establish a gradient of species richness (Leps 2004). Instead, it was advocated

564 to use extinction scenarios based on rarity of species (Grime 2002). However, with our

565 current knowledge, at least for subtropical forest ecosystems as the ones studied here, it seems

566 to be the best strategy to assemble communities randomly from the regional species pool.

567

23

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747

748 Table 1: Correlation coefficients of (A) variables describing plot characteristics and structure

749 and (B) variables describing species diversity of the different strata and life forms with the

750 first and second axis of the NMDS ordination. r^2 shows the proportion of variance explained

751 and p refers to the significance of the correlation between the variables in either set (A) or (B)

752 and the NMDS scores, based on a permutation test of (n=999). Significance codes '***' ≤

753 0.001 ; '**' ≤ 0.01 ; '*' ≤ 0.05.

A. Plot characteristics	Abbreviation in Fig. 2	NMDS1	NMDS2	r^2	p	
Successional stage	Successional_stage	0.997	0.079	0.616	0.001	***
Age of the 5th but largest tree [years]	Tree_age_max5	0.968	0.252	0.405	0.007	**
Elevation [m a.s.l.]	Elevation	0.135	0.991	0.780	0.001	***
Location in the NNR [Degrees N °]	Coordinates_N	-0.143	0.990	0.319	0.012	*
Location in the NNR [Degrees E °]	Coordinates_E	0.947	0.320	0.395	0.003	**
Eastness = sin(aspect [°])	Aspect_E	-0.880	-0.475	0.185	0.095	.
Northness = cos(aspect [°])	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	
Percentage of bare ground [%]	Open_soil	-0.803	0.596	0.110	0.226	
Soil moisture [g H_2O/g dry soil]	Soil_moisture	0.561	0.828	0.456	0.002	**
pH (0-5 cm) measured in H_2O	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) [%/%]	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	
Prop of recruit species new to a plot	Prop_exclusive_recruits	-0.740	-0.673	0.073	0.404	

754

755 Table 2: Results of univariate relationships of different response variables to successional

756 stage (columns on the left) or to the age of the fifth largest tree in a plot (columns on the

757 right). Significance codes '***' ≤ 0.001 ; '**' ≤ 0.01 ; '*' ≤ 0.05. Adult trees and shrubs

758 refers to individuals of > 1 m height, woody recruits to seedlings ≤ 1 m height.

Response variables	Successional stage (stage 1 to 5)				Age of the 5th but largest tree [yrs]			
	Slope	Correlation coefficient r	p		Slope	Correlation coefficient r	p	
Density of adult trees and shrubs (number per 30 x 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 x 30 m	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	

759

760

761 Table 3: Results of multiple regressions of species richness of adult trees and shrubs (> 1 m

762 height, not corrected for density of individuals) on predictor variables describing plot

763 characteristics and structure in the CSPs (for the full list of variables and abbreviations see

764 Table 1A). All variables were z transformed prior to analysis. Model selection was performed

765 with backward selection eliminating independent variables according to their F statistics, until

766 p was < 0.05 for all variables. p gives the probability values for the parameter estimates.

767 Partial r^2 is the partial variance explained using type II sum of squares. The whole model had

768 df = 4 with df = 23 for the error term, F = 5.27, p = 0.0037, r^2 = 0.478, adjusted r^2 = 0.388.

769

Variable	DF	Parameter Estimate	Standard Error	t value	p	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

770

771

772

773 **Captions**

774 Fig. 1: Study area. (A) Zhejiang (red), and Jiangxi (green) Provinces. (B) Kaihua county in

775 Zhejiang Province (red = area of Comparative Study Plots [CSPs] used for the study

776 reported in this paper), Dexing county in Jiangxi Province (green = area where an

777 associated forest biodiversity–ecosystem functioning experiment has been set up). (C)

778 Gutianshan NNR (red line) with CSPs (red dots) in Kaihua county (Zhejiang Province)

779 and the two associated experimental sites (green areas) in Dexing county, Jiangxi

780 Province.

781 Fig. 2: Definition of plot age classes. (A) Diameter at breast height (dbh) as a function of tree

782   age, across all Comparative Study Plots (CSPs) and all species. The solid line shows the

783   significant linear regression: dbh = 4.252 + 0.371 * age, r = 0.753, p < 0.001. (B) Age of

784   the fifth largest tree individual in the plot. The solid line shows the significant linear

785   regression: age = 17.39 – 15.52 * successional stage, r = 0.880, p < 0.001.

786   Fig. 3: Ordination of abundance of all adult tree and shrub species with at least one individual

787   > 1 m (n=148, black crosses) in the Comparative Study Plots (CSP, n=27, circles with

788   colors indicating the different successional stages, using non-metric multidimensional

789   scaling (NMDS). In various runs, a stable solution was found on average after four

790   random starts (stress = 15.86). (A) Post-hoc correlation of variables describing plot

791   characteristics and structure. (B) Post-hoc correlation of variables describing species

792   diversity of the different strata and life forms. See text for detailed methods and Table 1

793   for abbreviations and significance of correlations.

794   Fig. 4: Species richness based on 100 individuals (rarefaction) of adult trees and shrubs (> 1

795   m height) as a function of successional stage (1: < 20 yrs, 2: < 40 yrs, 3: < 60 yrs, 4: < 80

796   yrs, 5: ≥ 80 yrs). . The solid line shows the significant linear regression: r = 0.558, p =

797   0.003.

798   Fig. 5: Proportion of rare species calculated as ratio of number of rare species to number of all

799   species per plot as a function of successional stage (1: < 20 yrs, 2: < 40 yrs, 3: < 60 yrs, 4:

800   < 80 yrs, 5: ≥ 80 yrs). (A) Proportion of rare species among adult trees and shrubs (> 1 m

801   height): r = –0.078, p = 0.689. (B) Proportion of rare species among recruits (seedlings ≤

802   1 m): r = 0.158, p = 0.430.

803   Fig. 6: (A) Number of recruits as a function of number of adults for the 175 species that occur

804   in any of the plots as adult or recruit. Both variables were $\log_{10}(x+1)$ transformed. The

805   solid regression line gives the linear regression through the origin: y = 1.211 x, r^2 =

806   0.776, df = 174, p<0.0001. The broken line shows a line with slope = 1 for comparison,

807   assuming a per capita recruitment rate = 1 for all species. Confidence intervals are shown

808   as dotted lines and were plotted based on a tolerance of plus/minus two standard

809   deviations. (B) Log ratios of number of individuals in late successional stages (4 and 5) to

810   their number in early successional stages (1 and 2), log ratio of recruits regressed against

811   log ratio of adults. Confidence intervals are shown as dotted lines and were plotted based

812   on a tolerance of plus/minus 2 standard deviations. Species in the bottom left corner

813   (some of them marked in red) are those of which both adults and recruits prefer young

814   successional stages. Species in the top right corner (some of them marked in blue) are

815   those of which both adults and recruits prefer old successional stages. Species marked in

816   black are outliers, with recruits concentrated in other successional stages than adult

817   individuals (see text).

818 Fig. 7: Per capita recruitment rate per plot, calculated as average of per capita recruitment

819   rates of each species present as adults in a plot, as a function of proportion of rare species

820   in a plot, calculated as ratio of number of rare species to number of all species per plot: $r = 0.211$, $p = 0.291$.

821    $= 0.211$, $p = 0.291$.

822 Fig. 8: Similarity between species composition of adults and recruits based on counts of

823   individuals and the Bray-Curtis index as a function of successional stage (1: < 20 yrs, 2:

824   < 40 yrs, 3: < 60 yrs, 4: < 80 yrs, 5: ≥ 80 yrs): $r = -0.078$, $p = 0.701$.

825 Fig. 9: Proportion of recruit species new to a plot (no individual > 1 m height, i.e. exclusive

826   recruit species) as a function of species richness of adults of trees and shrubs (> 1 m

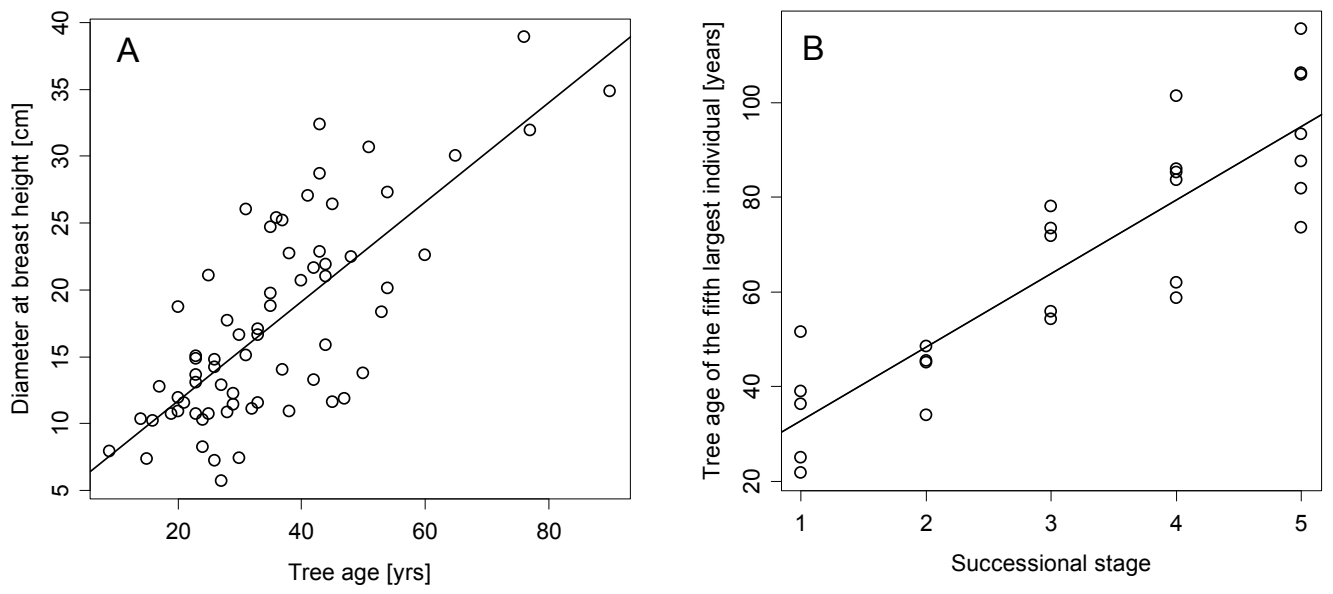827   height): $r = -0.549$, $p = 0.003$.

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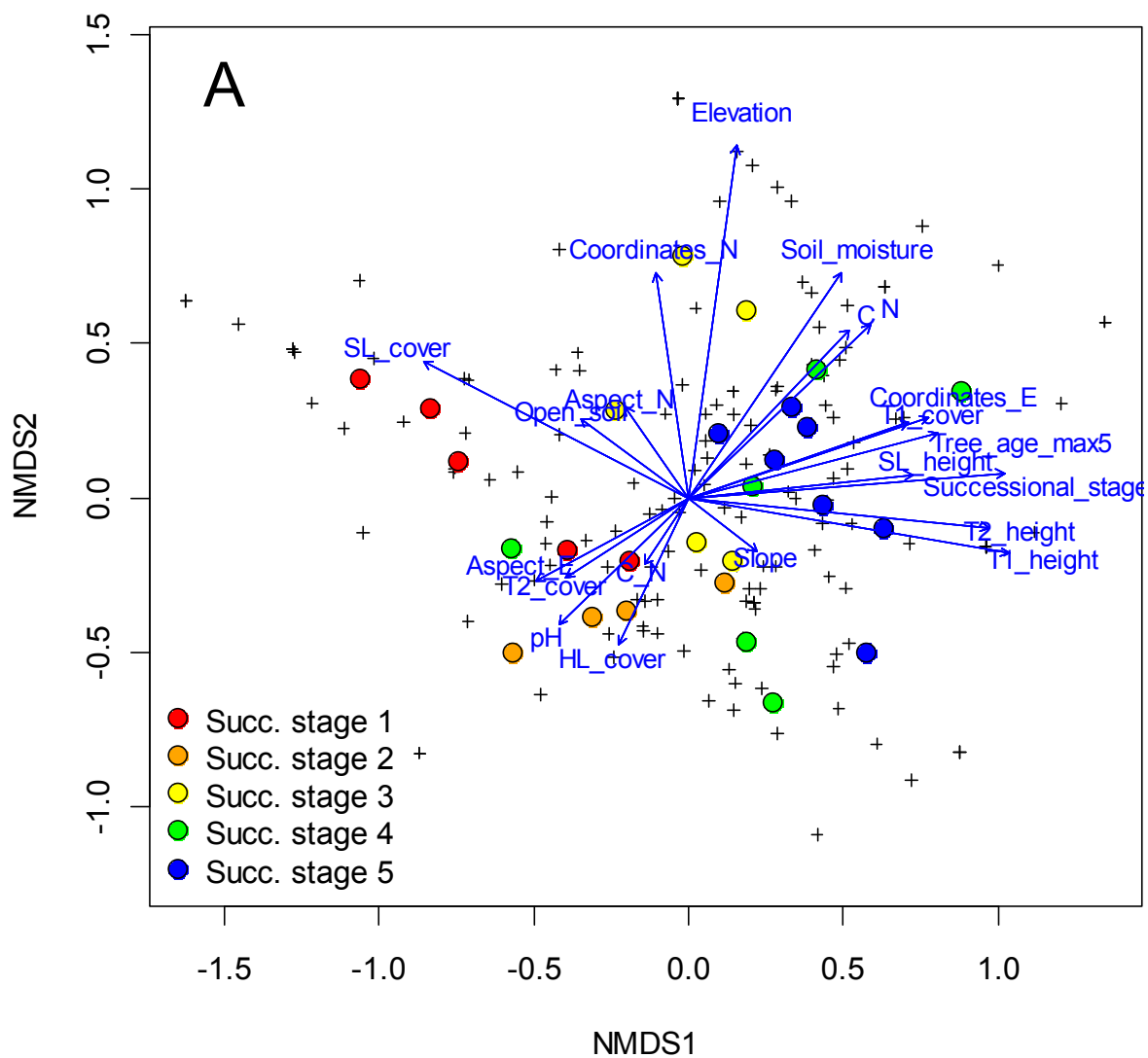
829 **Figures**
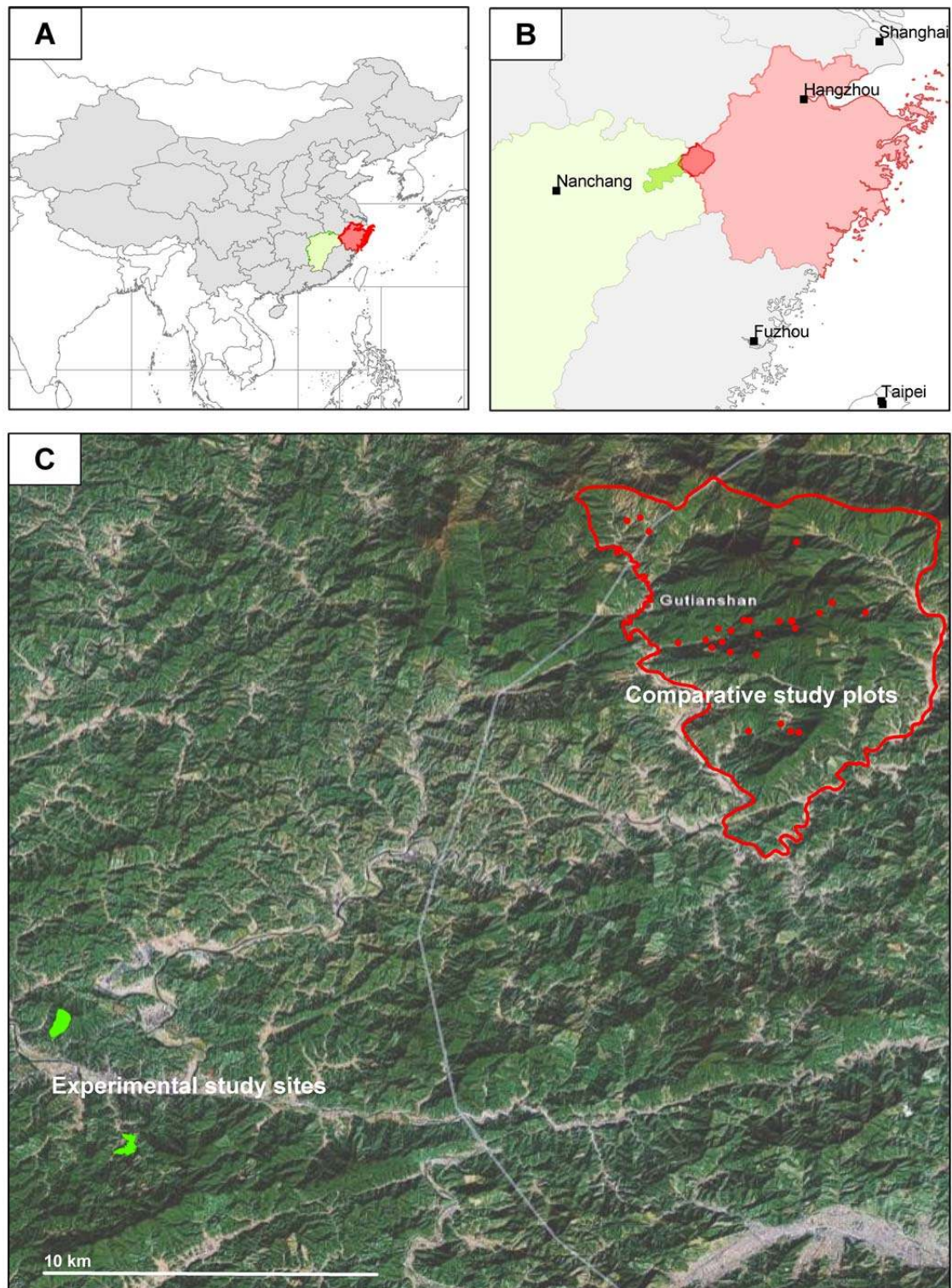
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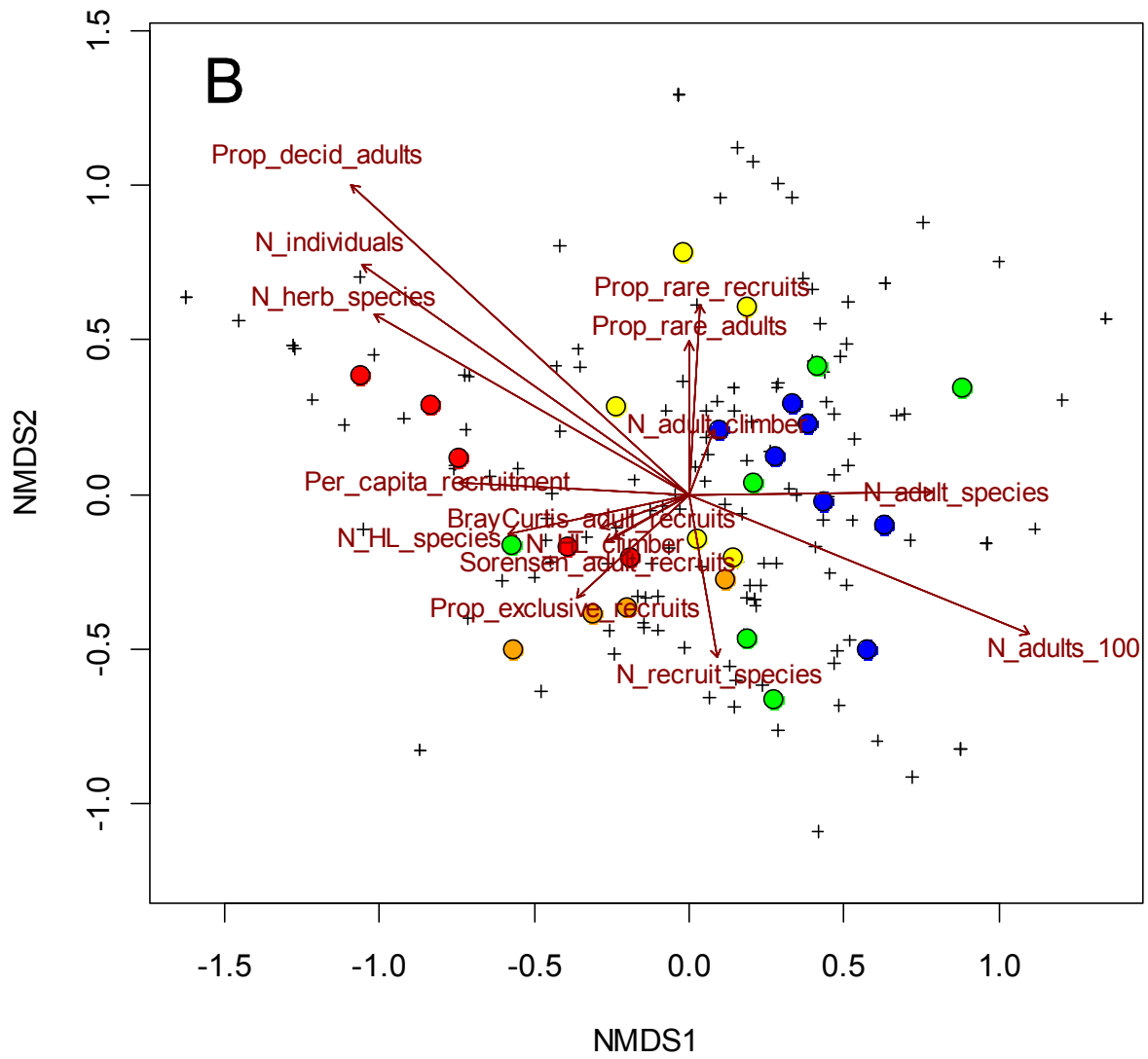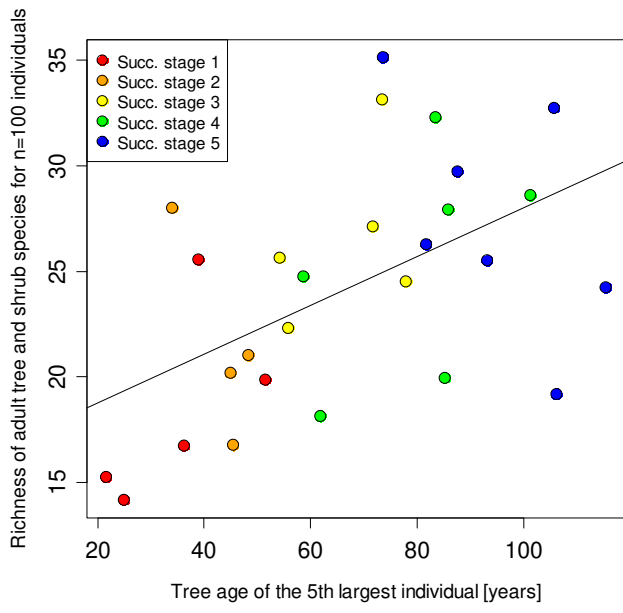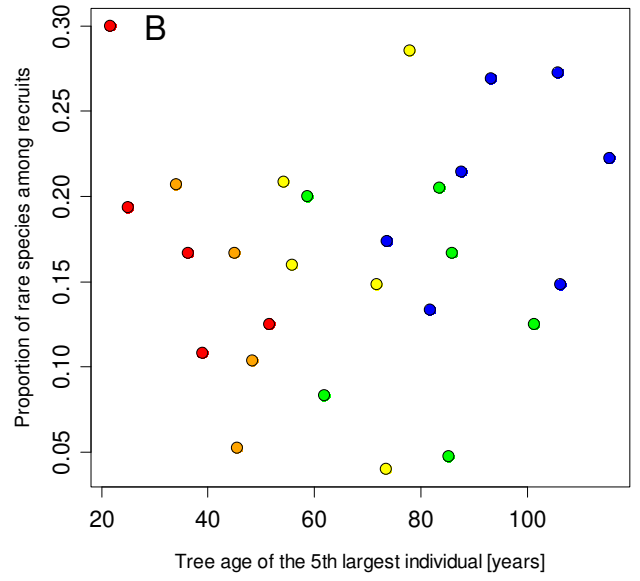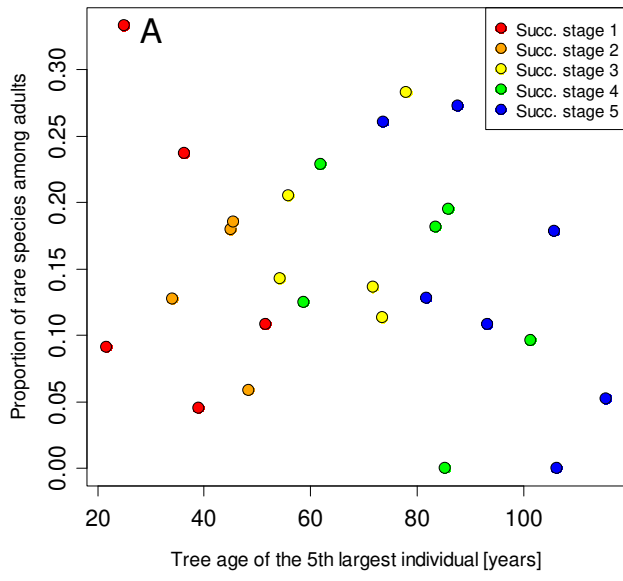831 Fig. 1

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834   Fig. 2

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Fig. 3A

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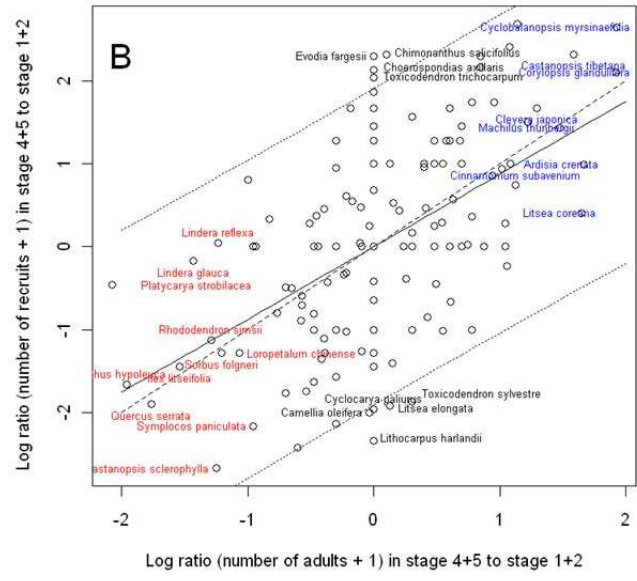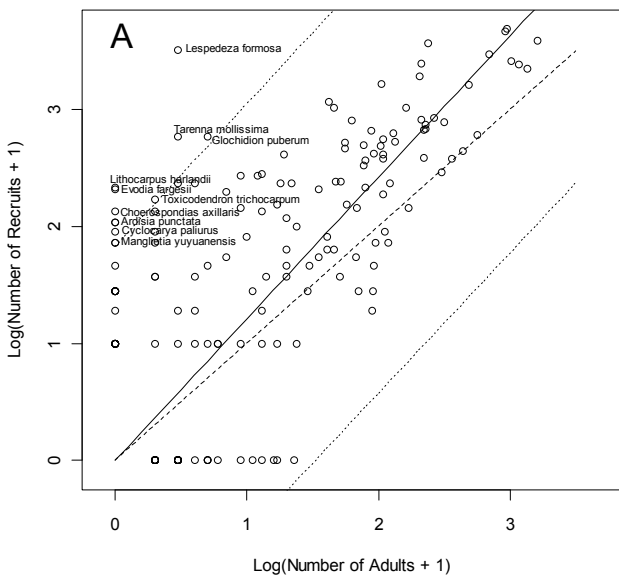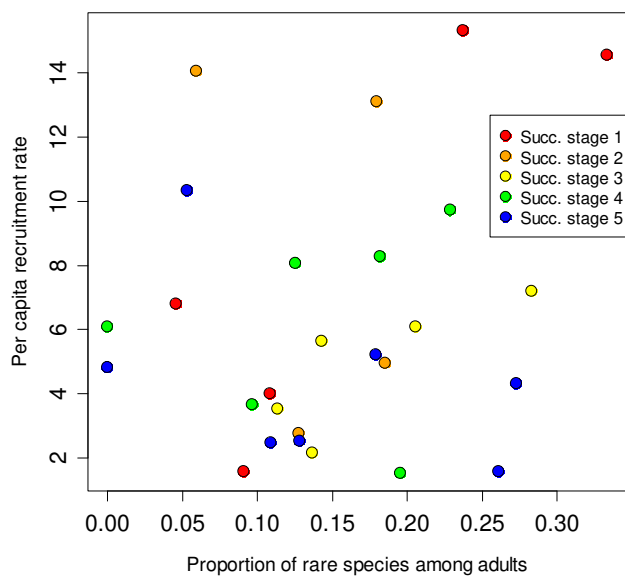2　Fig. 4

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Fig. 7

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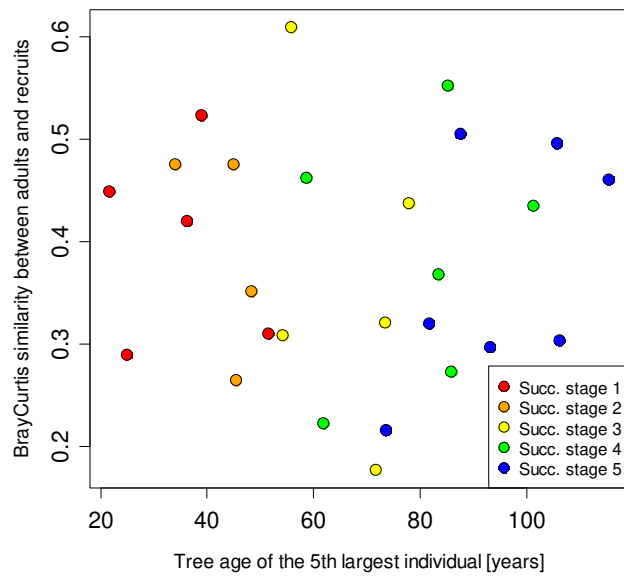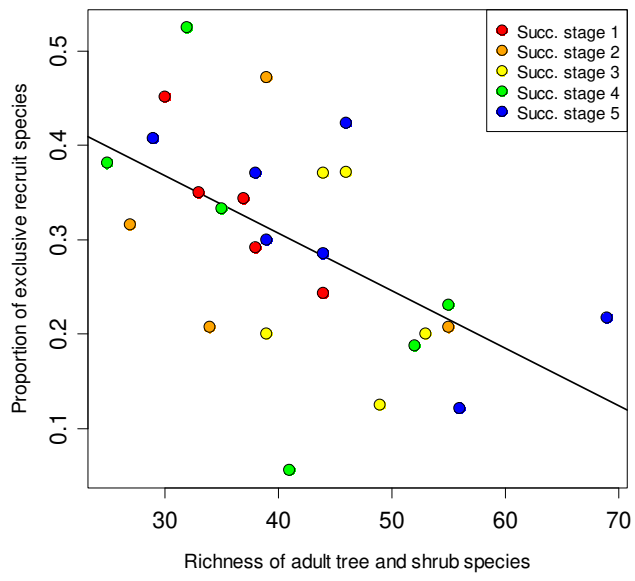
Fig. 9

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Appendix 1: List of all adult tree and shrub species (> 1 m height) encountered in the 27 Comparative Study Plots (CSPs) of the Gutianshan NRR. Species are listed with respect to the successional stage in which they occurred (1: < 20 yrs, 2: < 40 yrs, 3: < 60 yrs, 4: < 80 yrs, 5: ≥ 80 yrs). The first value in each column (shown in large letters) is percentage frequency, i.e. the number of plots in which a species occurred in this successional stage related to total number of plots in this group. The second column gives the Phi value as a measure of fidelity to the successional stage. Significant Phi values according to Fisher's exact test are underlined and printed in red color.

Successional stage	1		2		3		4		5	
Number of plots	5		4		5		5		7	

Concentrated in plots < 20 yrs

Species	Freq 1	Phi 1	Freq 2	Phi 2	Freq 3	Phi 3	Freq 4	Phi 4	Freq 5	Phi 5
Glochidion puberum (Linn.) Hutch.	60	<u>74.2</u>	.	---	.	---	.	---	.	---
Platycarya strobilacea Sieb. et Zucc.	80	<u>66.3</u>	50	27.9	.	---	.	---	.	---
Lindera glauca (Sieb. et Zucc.) Bl.	60	60.6	.	---	20	7.0	.	---	.	---
Lindera aggregata (Sims) Kesterm.	60	60.6	.	---	.	---	.	---	14	---
Symplocos paniculata (Thunb.) Miq.	60	60.6	.	---	20	7.0	.	---	.	---
Weigela japonica Thunb.	40	59.3	.	---	.	---	.	---	.	---
Camellia oleifera Abel	60	50.9	.	---	.	---	17	---	14	---
Litsea cubeba (Lour.) Pers.	60	50.9	50	33.8	.	---	.	---	.	---
Rhododendron mariesii Hemsl. et Wils.	40	43.8	.	---	20	13.5	.	---	.	---
Rhus hypoleuca Champ. ex Benth.	60	43.3	50	27.9	20	---	.	---	.	---
Sorbus folgneri (Schneid.) Rehd.	80	42.4	25	---	60	22.7	.	---	29	---
Lyonia ovalifolia (Wall.) Drude	80	42.4	25	---	60	22.7	17	---	14	---
Malus hupehensis (Pamp.) Rehd.	20	41.1	.	---	.	---	.	---	.	---
Hydrangea paniculata Siebold	20	41.1	.	---	.	---	.	---	.	---
Lindera erythrocarpa Makino	20	41.1	.	---	.	---	.	---	.	---
Betula luminifera Winkler	20	41.1	.	---	.	---	.	---	.	---
Viburnum sempervirens K. Koch	20	41.1	.	---	.	---	.	---	.	---
Albizia kalkora (Roxb.) Prain	100	39.5	75	13.4	40	---	50	---	43	---
Hydrangea chinensis Maxim.	80	38.1	.	---	60	18.7	17	---	43	2.5
Quercus serrata Murray	100	36.6	25	---	80	16.8	50	---	57	---
Rhododendron simsii Planch.	100	28.2	100	24.7	100	28.2	50	---	43	---
Liquidambar formosana Hance	60	27.0	50	14.7	40	6.7	17	---	14	---

Species					
Vaccinium bracteatum Thunb.	100 $^{25.5}$	100 $^{22.3}$	80 $^{2.5}$	67 $^{---}$	57 $^{---}$
Loropetalum chinense (R. Br.) Oliv.	100 $^{25.5}$	100 $^{22.3}$	60 $^{---}$	67 $^{---}$	71 $^{---}$
Pinus massoniana Lamb.	100 $^{25.5}$	75 $^{---}$	60 $^{---}$	67 $^{---}$	86 $^{11.3}$
Styrax odoratissima Champ.	80 $^{23.5}$	75 $^{16.3}$	40 $^{---}$	67 $^{12.0}$	29 $^{---}$
Nyssa sinensis Oliver	20 $^{22.9}$	. $^{---}$	. $^{---}$	17 $^{18.9}$	. $^{---}$
Photinia parvifolia (Prit.) Schneid.	40 $^{20.4}$	. $^{---}$	20 $^{---}$	33 $^{14.3}$	14 $^{---}$
Concentrated in plots < 40 yrs					
Diospyros kaki Thunb.	. $^{---}$	25 $^{47.0}$	. $^{---}$	. $^{---}$	. $^{---}$
Lespedeza formosa (Vogel.) Koehne.	. $^{---}$	25 $^{47.0}$	. $^{---}$	. $^{---}$	. $^{---}$
Cinnamomum camphora (Linn.) Presl	. $^{---}$	25 $^{47.0}$	. $^{---}$	. $^{---}$	. $^{---}$
Photinia hirsuta Hand.–Mazz.	. $^{---}$	25 $^{47.0}$	. $^{---}$	. $^{---}$	. $^{---}$
Rhamnus crenata Sieb. et Zucc.	. $^{---}$	25 $^{47.0}$	. $^{---}$	. $^{---}$	. $^{---}$
Ilex elmerrilliana S. Y. Hu	. $^{---}$	75 $^{41.4}$	20 $^{---}$	33 $^{4.3}$	29 $^{---}$
Lindera reflexa Hemsley	80 $^{26.9}$	100 $^{40.2}$	60 $^{7.8}$	17 $^{---}$	29 $^{---}$
Cyclobalanopsis glauca (Thunb.) Oers.	40 $^{---}$	100 $^{40.2}$	40 $^{---}$	33 $^{---}$	57 $^{6.3}$
Adinandra millettii (Hook. et Arn.) Ben. et Hook.	40 $^{---}$	100 $^{34.6}$	40 $^{---}$	83 $^{26.2}$	43 $^{---}$
Castanopsis carlesii (Hemsl.) Hayata	20 $^{---}$	75 $^{32.8}$	40 $^{2.9}$	33 $^{---}$	29 $^{---}$
Ilex pubescens Hook. et Arn.	. $^{---}$	50 $^{27.9}$	40 $^{20.4}$	17 $^{---}$	14 $^{---}$
Wikstroemia monnula Hance	. $^{---}$	25 $^{28.0}$	20 $^{22.9}$	. $^{---}$	. $^{---}$
Ilex litseifolia Hu et Tang	. $^{---}$	25 $^{28.0}$	. $^{---}$	17 $^{18.9}$	. $^{---}$
Tarenna mollissima Hook. et Arn.	. $^{---}$	25 $^{28.0}$	. $^{---}$	17 $^{18.9}$	. $^{---}$
Gardenia jasminoides Ellis	40 $^{15.3}$	50 $^{22.9}$	. $^{---}$	17 $^{---}$	29 $^{3.6}$
Chimonanthus salicifolius S. Y. Hu	. $^{---}$	25 $^{18.4}$	. $^{---}$	17 $^{9.4}$	14 $^{6.0}$
Concentrated in plots < 60 yrs					
Cyclobalanopsis stewardiana (Camus) Hsu et Jen	. $^{---}$	. $^{---}$	40 $^{59.3}$	. $^{---}$	. $^{---}$
Pinus taiwanensis Hayata	. $^{---}$	. $^{---}$	40 $^{59.3}$	. $^{---}$	. $^{---}$
Eurya alata Kobuski	20 $^{1.8}$	. $^{---}$	60 $^{50.9}$	. $^{---}$	14 $^{---}$
Litsea coreana Léveillé	. $^{---}$	. $^{---}$	100 $^{49.5}$	50 $^{2.0}$	71 $^{27.6}$
Viburnum erosum Thunb.	40 $^{---}$	. $^{---}$	100 $^{45.9}$	17 $^{---}$	86 $^{40.1}$
Photinia beauverdiana Schneid.	. $^{---}$	. $^{---}$	40 $^{43.8}$	17 $^{9.4}$	. $^{---}$
Dendropanax dentiger (Harms) Merr.	. $^{---}$	. $^{---}$	40 $^{43.8}$	. $^{---}$	14 $^{6.0}$
Michelia skinneriana Dunn	. $^{---}$	. $^{---}$	20 $^{41.1}$	. $^{---}$	. $^{---}$
Tilia endochrysea Hand.–Mazz.	. $^{---}$	. $^{---}$	20 $^{41.1}$	. $^{---}$	. $^{---}$
Ilex micrococca Maxim.	. $^{---}$	. $^{---}$	20 $^{41.1}$	. $^{---}$	. $^{---}$

Species					
Symplocos olongifolia Fletch.	. ---	. ---	20 $^{41.1}$	. ---	. ---
Styrax wuyuanensis Hwang	. ---	. ---	20 $^{41.1}$	. ---	. ---
Cornus kousa Buerger	. ---	. ---	20 $^{41.1}$	. ---	. ---
Sorbus dunnii Rehder	. ---	. ---	20 $^{41.1}$	. ---	. ---
Toxicodendron trichocarpum (Miquel) Kuntze	. ---	. ---	20 $^{41.1}$	. ---	. ---
Cyclobalanopsis nubium (Hand.–Mazz.) Chun	. ---	. ---	20 $^{41.1}$	. ---	. ---
Symplocos anomala Diels	20 ---	50 $^{4.7}$	80 $^{34.1}$	50 $^{6.0}$	29 ---
Elaeocarpus japonicus Sieb. et Zucc.	. ---	25 $^{12.0}$	40 $^{33.8}$	. ---	14 ---
Symplocos stellaris Diels	20 ---	75 $^{4.2}$	100 $^{30.9}$	83 $^{15.2}$	71 $^{1.4}$
Rhaphiolepis indica (Linn.) Lindl.	60 ---	100 $^{24.7}$	100 $^{28.2}$	67 ---	57 ---
Prunus schneideriana Koehne	. ---	. ---	40 $^{26.4}$	17 ---	29 $^{15.3}$
Prunus campanulata Maxim.	. ---	. ---	20 $^{22.9}$	17 $^{18.9}$	. ---
Cyclobalanopsis gracilis (Re. et Wi.) Cheng et Hon	. ---	. ---	20 $^{22.9}$	17 $^{18.9}$	. ---
Symplocos setchuensis (Thunb.) Sieb. et Zucc.	. ---	. ---	20 $^{22.9}$	17 $^{18.9}$	. ---
Carpinus viminea Lindl.	. ---	. ---	20 $^{22.9}$	. ---	14 $^{15.5}$
Hovenia trichocarpa Chun et Tsiang	. ---	. ---	20 $^{22.9}$	. ---	14 $^{15.5}$
Castanopsis fargesii Franchet	20 ---	25 ---	60 $^{22.7}$	50 $^{14.3}$	29 ---
Quercus phillyreoides Gray	. ---	25 $^{2.8}$	40 $^{20.4}$	17 ---	29 $^{9.0}$

Concentrated in plots < 80 yrs

Species					
Styrax dasyanthus Perkins	. ---	25 ---	20 ---	67 $^{49.7}$	14 ---
Clerodendrum cyrtophyllum Turcz.	. ---	. ---	. ---	33 $^{37.8}$	14 $^{6.0}$
Pieris formosa (Wall.) Don	. ---	. ---	. ---	17 $^{36.7}$	. ---
Sapium japonicum (Sieb. et Zucc.) Pax. et Hoffm.	. ---	. ---	. ---	17 $^{36.7}$	. ---
Diospyros japonica Sieb. et Zucc.	. ---	. ---	20 $^{7.0}$	33 $^{27.9}$	14 ---
Meliosma oldhamii Miquel	40 ---	50 ---	80 $^{16.8}$	83 $^{22.5}$	57 ---
Acer pubipalmatum Fang	. ---	. ---	. ---	17 $^{36.7}$	. ---
Symplocos heishanensis Hayata	. ---	. ---	. ---	17 $^{36.7}$	. ---
Schoepfia jasminodora Sieb. et Zucc.	. ---	. ---	. ---	17 $^{36.7}$	. ---
Ilex suaveolens (Léve.) Loes.	. ---	. ---	. ---	17 $^{36.7}$	. ---
Elaeocarpus chinensis (Gard. et Champ.) Hook.	20 ---	25 $^{2.8}$	. ---	50 $^{35.7}$	14 ---
Cinnamomum subavenium Miquel	. ---	25 ---	40 ---	67 $^{28.2}$	57 $^{19.7}$
Ilex chinensis Sims	. ---	. ---	. ---	17 $^{18.9}$	14 $^{15.5}$
Cephalotaxus fortunei Hooker	. ---	. ---	. ---	17 $^{18.9}$	14 $^{15.5}$
Elaeocarpus decipiens Hemsley	. ---	. ---	. ---	17 $^{18.9}$	14 $^{15.5}$

Species	P1		P2		P3		P4		P5	
Premna microphylla Turc.	.	---	.	---	.	---	17	18.9	14	15.5
Concentrated in plots ≥ 80 yrs										
Photinia glabra Maxim.	20	---	.	---	40	---	33	---	86	54.2
Castanopsis tibetana Hance	.	---	25	2.8	20	---	.	---	57	49.7
Ardisia crenata Sims	.	---	.	---	.	---	33	14.3	57	49.7
Ternstroemia gymnanthera (Wight et Arn.) Bedd.	.	---	75	13.4	20	---	83	26.2	100	49.1
Toxicodendron succedaneum (Linn.) Kuntze	20	---	75	13.4	60	---	33	---	100	49.1
Ilex buergeri Miquel	.	---	50	11.2	20	---	33	---	71	42.1
Mahonia bealei (Fort.) Carr.	.	---	.	---	.	---	.	---	29	47.8
Machilus thunbergii Sieb. et Zucc.	20	---	25	---	100	33.7	67	---	100	41.8
Alangium kurzii Craib	.	---	.	---	.	---	33	20.4	43	37.1
Osmanthus cooperi Hemsley	.	---	25	7.0	20	1.8	.	---	43	37.1
Camellia chekiang-oleosa Hu	20	---	.	---	40	---	50	10.1	71	36.9
Daphniphyllum oldhamii Hemsley	20	---	25	---	60	4.3	67	12.0	86	35.9
Neolitsea aurata (Hay.) Koid.	.	---	50	---	80	23.5	50	---	86	35.9
Cyclobalanopsis myrsinaefolia Oerst.	.	---	.	---	20	---	50	23.8	57	35.6
Rhododendron latouchea Franchet	80	6.4	25	---	80	6.4	67	---	100	35.0
Tricalysia dubia (Lindl.) Ohwi	.	---	.	---	.	---	.	---	14	33.1
Toxicodendron sylvestre (Sieb. et Zucc.) Kunt.	.	---	.	---	.	---	.	---	14	33.1
Idesia polycarpa Maxim.	.	---	.	---	.	---	.	---	14	33.1
Randia cochinchinensis (Lour.) Merr.	.	---	.	---	.	---	.	---	14	33.1
Euonymus centidens Léveillé	.	---	.	---	.	---	.	---	14	33.1
Pieris japonica (Thunb.) Don	.	---	.	---	.	---	.	---	14	33.1
Picrasma quassioides (Don) Benn.	.	---	.	---	.	---	.	---	14	33.1
Ficus sarmentosa Buch.–Hamil.	.	---	.	---	.	---	.	---	14	33.1
Prunus discoides Yu et Li	.	---	.	---	.	---	.	---	14	33.1
Vernicia montana Loureiro	.	---	.	---	.	---	.	---	14	33.1
Lauracerasus spinulosa (Sieb. et Zucc.) Schneid.	.	---	25	18.4	.	---	.	---	29	32.9
Corylopsis glandulifera Hemsley	.	---	.	---	40	6.7	50	18.9	57	29.9
Acer cordatum Pax	.	---	.	---	20	---	33	14.3	43	29.4
Litsea elongata Hook.	20	---	.	---	.	---	33	14.3	43	29.4
Lithocarpus glaber (Thunb.) Nakai	40	---	100	19.9	60	---	100	25.5	100	28.2
Camellia fraterna Hance	40	---	50	---	60	---	67	4.1	86	27.9
Fraxinus insularis Hemsley	20	---	50	11.2	40	2.9	17	---	57	24.6

Species	C1		C2		C3		C4		C5	
Meliosma flexuosa Pamp.	.	---	25	12.0	.	---	17	2.8	29	22.9
Ilex wilsonii Loes.	.	---	.	---	20	7.0	17	2.8	29	22.9
Malus leiocalyca Huang	20	7.0	.	---	.	---	17	2.8	29	22.9
Acer amplum Rehder	.	---	.	---	20	7.0	17	2.8	29	22.9
Machilus pauhoi Kanehira	.	---	.	---	20	7.0	17	2.8	29	22.9
Cleyera japonica Thunb.	.	---	25	---	60	18.7	50	10.1	57	19.7
Ilex purpurea Miquel	20	---	50	---	60	4.3	67	12.0	71	18.9
Species without any preference										
Schima superba Gardn. et Champ.	100	---	100	---	100	---	100	---	100	---
Eurya muricata Dunn	100	---	100	---	100	---	100	---	100	---
Vaccinium mandarinorum Diels	100	9.3	100	8.2	100	9.3	83	---	100	11.6
Castanopsis eyrei (Champ. ex Benth.) Tutch.	80	---	100	8.2	100	9.3	100	10.5	100	11.6
Myrica rubra Sieb. et Zucc.	80	---	100	14.7	80	---	83	---	100	20.9
Eurya rubiginosa Chang	80	13.5	50	---	80	13.5	50	---	71	6.0
Symplocos sumuntia Buch.-Ham.	80	23.5	50	---	60	4.3	67	12.0	29	---
Vaccinium carlesii Dunn	60	---	100	17.4	100	19.9	83	---	86	---
Cunninghamia lanceolata (Lamb.) Hook.	60	18.7	25	---	60	18.7	33	---	29	---
Castanea henryi (Skan) Rehd. et Wils.	60	14.9	25	---	40	---	33	---	57	15.1
Rhododendron ovatum (Lindl.) Planch.	40	---	75	---	100	19.9	100	22.3	100	24.7
Machilus grijsii Hance	40	---	75	29.1	40	---	50	10.1	14	---
Syzygium buxifolium Hook. et Arno.	40	---	75	16.3	40	---	50	---	71	18.9
Dalbergia hupeana Hance	40	---	50	7.9	60	18.7	33	---	29	---
Itea chinensis Hook. et Arno.	40	---	50	1.5	40	---	50	2.0	57	10.6
Euscaphis japonica (Thunb.) Kanitz	40	6.7	25	---	40	6.7	33	---	29	---
Ilex rotunda Thunb.	20	---	25	---	40	---	50	6.0	71	32.1
Serissa serissoides Druce	40	33.8	.	---	40	33.8	.	---	.	---
Castanopsis sclerophylla (Lindl. et Pax.) Schott.	20	7.0	.	---	20	7.0	17	2.8	14	---
Alniphyllum fortunei (Hemsl.) Makino	.	---	50	18.6	40	10.8	33	4.3	29	---
Magnolia cylindrica Wilson	.	---	.	---	20	13.5	17	9.4	14	6.0
UNIDENTIFIED SPECIES	40	---	75	4.2	80	10.1	83	15.2	71	1.4