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# A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China

GUOYI ZHOU*, CHANGHUI PENG†‡, YUELIN LI*, SHIZHONG LIU*, QIANMEI ZHANG*, XULI TANG*, JUXIU LIU*, JUNHUA YAN*, DEQIANG ZHANG* and GUOWEI CHU*

**South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, 510650, China, †Department of Biology Sciences, Institute of Environment Sciences, University of Quebec at Montreal, C.P. 8888, Succ. Centre-Ville, Montreal, Canada, H3C 3P8, ‡Laboratory for Ecological Forecasting and Global Change, College of Forestry, Northwest A & F University, Yangling, Shaanxi 712100, China*

## Abstract

Recent studies have suggested that tropical forests may not be resilient against climate change in the long term, primarily owing to predicted reductions in rainfall and forest productivity, increased tree mortality, and declining forest biomass carbon sinks. These changes will be caused by drought-induced water stress and ecosystem disturbances. Several recent studies have reported that climate change has increased tree mortality in temperate and boreal forests, or both mortality and recruitment rates in tropical forests. However, no study has yet examined these changes in the subtropical forests that account for the majority of China's forested land. In this study, we describe how the monsoon evergreen broad-leaved forest has responded to global warming and drought stress using 32 years of data from forest observation plots. Due to an imbalance in mortality and recruitment, and changes in diameter growth rates between larger and smaller trees and among different functional groups, the average DBH of trees and forest biomass have decreased. Sap flow measurements also showed that larger trees were more stressed than smaller trees by the warming and drying environment. As a result, the monsoon evergreen broad-leaved forest community is undergoing a transition from a forest dominated by a cohort of fewer and larger individuals to a forest dominated by a cohort of more and smaller individuals, with a different species composition, suggesting that subtropical forests are threatened by their lack of resilience against long-term climate change.

*Keywords:* Ecological resilience, Growth trends, Mortality and recruitment, Species composition, Subtropical forests, Warming and drying environment

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## Introduction

Climate change is threatening tropical forest communities in a variety of ways, such as increasing the frequency of severe droughts, large fires, storms, and flooding (Davidson *et al*., 2012). Ecological resilience is the ability of an ecosystem to return to its original state following a perturbation, thereby maintaining its essential characteristic taxonomic composition, structures, ecosystem functions, and rates of key processes (Folke *et al*., 2004; Walker *et al*., 2004). The resilience of a forest ecosystem against changing climatic conditions is determined by its biological resources, species composition, and ecological functions. Resilience is also influenced by the size of the forest ecosystem (generally, larger and less fragmented forests are more resilient), and by the condition and characteristics of the surrounding landscape (Scheffer *et al*., 2009). One of the main results predicted to occur as a result of global climate change is a combination of rising temperatures and increased water stress (Luo *et al*., 2008; Zhou *et al*., 2011), which will exert an unavoidable negative impact on ecosystem resilience (IPCC, 2007; Malhi *et al*., 2009; Enquist & Enquist, 2011). Several studies have documented that regional warming and the resulting increase in drought stress have caused vegetation shifts (Allen & Breshears,1998), increased tree mortality (Mueller *et al*., 2005; van Mantgem & Stephenson, 2007; McDowell *et al*., 2008; Breshears *et al*., 2009; van Mantgem *et al*., 2009; Peng *et al*., 2011), decreased tree diameter growth (Clark *et al*., 2003, 2010; Feeley *et al*., 2007; da Costa *et al*., 2010), decreased biomass carbon sinks (Ciais *et al*., 2005; Phillips *et al*., 2009; Ma *et al*., 2012), and increased die-off of some species (Breshears *et al*., 2005). When tree mortality rates have increased,

Correspondence: Guoyi Zhou, South China Botanical Garden, Chinese Academy of Sciences, No 723, Xingke Road, Tianhe District, Guangzhou, 510650, China, tel. + 86 20 3725 2708, fax + 86 20 3725 2615, e-mail: gyzhou@scib.ac.cn

the recruitment rates remained either unchanged (e.g. in temperate old-growth forests; van Mantgem & Stephenson, 2007; van Mantgem *et al.*, 2009) or increased in parallel with increasing mortality rates (e.g. in tropical old-growth forests; Lewis *et al.*, 2004a; Phillips *et al.*, 2004). Such studies are important not only for identifying the ecological resilience against climate change, but also for evaluating changes in ecosystem services, because persistent changes in tree size, productivity, and mortality rates could presage substantial alterations in forest structure and composition (van Mantgem *et al.*, 2009), leading to changes in forest functions and in ecosystem resilience (Engelbrecht *et al.*, 2007). Identifying the degree of ecological resilience against climate change is a big challenge because of the inherent complexity of climate systems and the problem of short-term fluctuations that may be mistaken for long-term trends (Willis *et al.*, 2010). The use of long-term forest monitoring plots, which provides data on combinations of abiotic and biotic processes, could provide valuable evidence for and helpful insights into ecological resilience under a changing climate (Walker *et al.*, 2004).

Monsoon evergreen broad-leaved forest is the climax vegetation type of subtropics and the product of long-term effects of a monsoon climate. Long-term changes in the vegetation's structure and composition may reflect changes of the climatic traits in the region that drive the formation of the climax vegetation. Recent progress has been made in assessing the impact of changes in precipitation and temperature patterns on the responses of hydrological regimes in these forests to climate change and on the underlying mechanisms responsible for their interactions (Zhou *et al.*, 2010, 2011), as well as on other ecosystem processes in old-growth forests (Tang *et al.*, 2006, 2011; Yan *et al.*, 2006; Zhou *et al.*, 2006a,b, 2007; Mo *et al.*, 2008). Zhou *et al.* (2011) noted that with rising air temperatures in southern China since 1980, rainfall patterns have shifted toward more severe storms during the wet season, more rain-free days during the year, and fewer days per year with light rain, even though total rainfall did not change significantly. As a result, soil moisture during the dry season has shown a significant decreasing trend, and extreme hydrological events (e.g. droughts and floods) have become more frequent and severe.

How would the characteristics of forest communities change under such a warming and drying environment? To our knowledge, no study has used long-term forest observation plots to directly examine the responses of forest communities to recent climate change in the region. In this article, we used data from eight surveys of permanent observation plot in a climax monsoon evergreen broad-leaved forest between 1978 and 2010 to investigate if the directional changes in age composition, biomass, tree quantity, diameter growth rates, mortality and recruitment rates, and species quantity have occurred in the past decades and examine if the directional changes are resulted from global warming and the consequent soil dryness. The forest in which we established the permanent plots has had no disturbance for more than 400 years (Zhou *et al.*, 2006a).

## Materials and methods

### Region and community descriptions

The Dinghushan Biosphere Reserve (23°09′21″N–23°11′30″N, 112°32′39″E–112°35′41″E) is located about 84 km west of Guangzhou city in central Guangdong Province of southern China. It was established in 1950 to protect natural monsoon evergreen broad-leaved forests in the southern subtropics and was accredited as China's first National Natural Reserve in 1956. The region has a typical southern subtropical monsoon climate, with annual average precipitation of 1678 mm, of which nearly 80% falls during the wet season (April–September) and the other 20% falls during the dry season (October–March). The annual mean temperature and relative humidity are 22.3 °C and 77.7%, respectively. The lowest mean monthly temperature is 13.9 °C in January and the highest is 28.9 °C in August. The bedrock is sandstone and shale. Soils, with pH-values ranging from 4.0 to 4.9, are classified in the ultisol group and the udult subgroup according to the USDA soil classification system (Buol *et al.*, 2003). The soil profile usually ranges from 50 to 80 cm in depth.

Dinghushan is regarded as a sacred mountain by local people as well as all Cantonese due to the Buddhist temple that has existed there for more than 1300 years. Annual records from the temple showed that no permission was granted for any removal of plants (logging) or grazing. Monsoon evergreen broad-leaved forest, close to the Buddhist temple, is distributed in the core area of the reserve and has not been disturbed for more than 400 years. A series of studies was done to demonstrate that the forest has not been disturbed for that long. Charcoal in soils and tree stumps with fire scars have not been found since the first survey in 1978. A $^{14}$C dating study showed that the forest soil has not been disturbed for more than 400 years (Shen *et al.*, 1999). Studies of forest succession also demonstrated that the present state of the monsoon evergreen broad-leaved forest has been maintained for more than 400 years (Wang & Ma, 1982). An 8-ha experimental site was established at an altitude of 200–300 m on a south-facing slope, and we established a 1-ha permanent sample plot toward the center of this site in 1978. Studies have demonstrated that the permanent plot successfully represented the species diversity of monsoon evergreen broad-leaved forest and contained about 80 tree species in 1978 (Wang & Ma, 1982). The dominant tree species includes *Castanopsis chinensis* Hance, *Schima superba* Gardn. et Champ, *Canarium album* (Lour.) Rauesch, *Gironniera subaequalis* Planch, with heights ranging from 14 to 25 m. The dominant shrub species includes *Psychotria rubra* (Lour). Poir and *Blastus cochinchinensis* Lour, with heights <5 m. Table S1 (Supporting Information) provides a detailed description of the dominant taxa and key aspects of the ecosystem's functioning.

### Community surveys

We surveyed the tree community in 1978, 1982, 1992, 1994, 1999, 2004, 2008, and 2010. All individuals with a diameter at breast height (DBH at 1.3 m above the ground) $\geq 1$ cm and a height $\geq 1.5$ m in the permanent sample plot were labeled in 1978. Any newly recruited individuals that met these criteria were also labeled in the subsequent surveys. Each individual was assigned a unique number. Due to damage to the labels between 1982 and 1992, all individuals were newly labeled in 1992. Unfortunately, it was rarely possible to establish the relationship between the old labels and the new labels, so we could not reliably connect an individual's histories before and after 1992. Since 1992, all individuals have been accurately traced. We have therefore emphasized the data collected since 1992 in our analysis. During each survey, we identified the species and status (disease and insect status; suppressed or dominant; health conditions) of each labeled individual. We also measured the DBH, height, and spatial coordinates of all labeled individuals. The spatial coordinates were recorded to a two-dimensional accuracy of ±15 cm using tape rulers.

Measurements of DBH and height for each individual were used to calculate aboveground and belowground biomass using the empirical allometric relationships established by Wen *et al.* (1997) and Tang *et al.* (2011) in another plot in the same forest. To identify the changes in community structure and biomass, we divided all individuals into four DBH classes (1 cm $\leq$ DBH $\leq$ 5 cm, 5 cm < DBH $\leq$ 10 cm, 10 cm < DBH $\leq$ 20 cm, and DBH > 20 cm) and four functional groups: tall tree (>16 m in height), intermediate tree (10–16 m in height), short tree (5–10 m in height), and shrub (1.5–5 m in height). We classified each species into one of those four functional groups based on the height of a mature individual of that species, which we based on the height data for that species in the Flora of China (Institute of Botany, Chinese Academy of Sciences, 2005). That is, if a species belongs to the tall tree category (its mature individuals are taller than 16 m), immature individuals of the species also belong to the tall tree category, even if they are shorter than 16 m at the time of the survey.

### Mortality and recruitment rates

We defined the relative mortality rate, $RMR(i,j)$ (in% yr$^{-1}$), for DBH class or functional group $i$ ($i$ = 1–4 for both DBH and functional group) in period $j$ = 1 (1992–1994), 2 (1994–1999), 3 (1999–2004), 4 (2004–2008), or 5 (2008–2010) as the number of individuals that died between two successive surveys, $D(i, j)$, divided by the number of individuals that were alive at the start of that period, $N(i, j)$, and by the time interval, $\Delta t_j$ (years):

$$RMR(i,j) = \frac{D(i,j)}{N(i,j)\Delta t_j} \times 100\% \tag{1}$$

For the same DBH or functional group classes and the same periods used for the mortality rate, we defined the relative recruitment rate, $RRR(i,j)$ (in% yr$^{-1}$), as the number of new individuals at the end of a period, $R(i, j)$, divided by the number of individuals that were present at the start of the period, $N(i, j)$, and by the time interval, $\Delta t_j$ (years):

$$RRR(i,j) = \frac{R(i,j)}{N(i,j)\Delta t_j} \times 100\% \tag{2}$$

The census intervals ($\Delta t_j$) used for estimating mortality and recruitment rates were 2, 4, and 5 years in this article. Usually, the estimated rates of mortality and recruitment will decrease with increasing census interval in censuses of nonhomogeneous populations. Lewis *et al.* (2004b) suggested that the underestimation percentages for intervals of 2, 4, and 5 years were 5.7%, 11.7%, and 13.7%, respectively. The underestimation percentages for 4- and 5-year intervals are therefore 6% and 8% points, respectively, higher than that for the 2-year interval. This is not sufficiently large to distort the temporal sequence of mortality and recruitment rates calculated in this article. Thus, to simplify our analysis and facilitate comparison with other studies that did not correct for the census interval, we have reported the original rates here.

Because all individuals were newly labeled in 1992 and the label number of individuals differed before and after 1992, the surveys in 1978 and 1982 were not included in calculating the relative mortality and recruitment rates to minimize the risk of incorrect results.

### DBH growth rate

Because of the above-mentioned labeling problem, we did not include the 1978 and 1982 surveys in our calculations of the DBH growth rates. Furthermore, to minimize the risk of incorrect results and to improve the consistency and precision of our analysis, we used all 1337 individuals that remained alive throughout the 1992–2010 census period to calculate the DBH growth rates (*DGR*) in different census periods.

DBH growth rates in DBH class or functional group $i$ during period $j$, $DGR(i, j)$, was calculated as follows:

$$DGR(i,j) = \frac{\sum_{k=1}^{N} \Delta DBH(i,j)_k}{N\Delta t_j} \tag{3}$$

where $\Delta DBH(i, j)_k$ is the DBH increment (mm) of individual $k$ ($k$ = 1, 2,…, $N$) that belongs to DBH class or functional group $i$ during period $j$, and $\Delta t_j$ is the time interval (years) for period $j$.

### Estimation of the age composition of the forest community

To estimate the contribution of age effects to DBH growth, we calculated the DBH growth rates in a different way, as the arithmetic-mean DBH growth rate (*ADGR*). *ADGR* was calculated as follows:

$$ADGR_i = \frac{DBH_{i,2010} - DBH_{i,1992}}{18} \quad (4)$$

where $ADGR_i$ is the average DBH growth rate of individual $i$ ($i$ = 1, 2, 3, …, 1337, which includes all individuals that remained alive throughout the study period from 1992 to 2010). $DBH_{i,1992}$ and $DBH_{i,2010}$ represent the DBH of individual $i$ in 1992 and 2010, respectively, and 18 represents the duration (years) of the calculation period.

Although this approach can only partly eliminate the environment's effects on DBH growth, it remains one of the most practical and frequently used approaches to estimate the contribution of endogenous factors to DBH growth in a natural environment.

After obtaining the *ADGR* through Eqn (4), we fitted the curve of ADGR~DBH that can be used to estimate the age composition of the forest according to the following procedures:

(i) Arranging all individuals in order from the smallest DBH to the largest DBH and numbered each individual as $i$ ($i$ = 1,2, …, all individuals of the plot), so that $DBH_0$ equals to 1 cm and $DBH_{i-1} \leq DBH_i$.
(ii) Estimating the ages of all individuals (years) using iterative method as follows:

$$\begin{cases} A_0 = 1 \\ A_i = A_{i-1} + \frac{DBH_i - DBH_{i-1}}{ADGR_i} \end{cases} \quad (5)$$

where $DBH_i - DBH_{i-1}$ represents the DBH difference between the two adjacent individuals in the order from the smallest DBH to the largest DBH; $ADGR_i$ is the DBH growth rate between $DBH_{i-1}$ and $DBH_i$ in the curve of ADGR~DBH; $A_0$ was assumed to be 1 (year); $A_i$ is the age for the individual (s) of $DBH_i$; $A_{i-1}$ is the age for the individual(s) of $DBH_{i-1}$.

### *Sap flow measurements*

We used Granier's (1987) thermal dissipation probe method to measure sap flow in the trees. Close to the permanent plot, we randomly selected three locations with each area being 1000 m$^2$ and installed probes (DL2e probes with LAC-1 input cards in single-ended mode; Delta-T Devices, Cambridge, England) in trees of various diameters. Widths of the wounds due to installation of probes were measured through implanting 'dummy' probes (nonfunctioning probes) into several nearby trees and monitoring the change in wound size with time. The instrument and data loggers were directly powered by batteries. At each location, we selected 17 trees with DBH ranging from 12 to 45 cm based on field surveys, representing the main DBH ranges of mature individuals for the functional groups of tall tree and intermediate tree on the studied plot. The selected trees distributed in the whole location. The measurements began in April 2008 and have been continuous since then. Information was recorded at half hour intervals, corrected for wound size (Steppe *et al.*, 2010) and transformed into an instantaneous sap flow density (*SFD*, g $H_2O$ m$^{-2}$ s$^{-1}$) at that time (for example, 7:00, 7:30, …, 18:30, 19:00) using the following equation (Granier, 1987):

$$SFD = 119 \times [(\Delta T_{\max} - \Delta T)/\Delta T]^{1.231} \quad (6)$$

where $\Delta T_{\max}$ is the maximum temperature difference between day and night for the two sensors; $\Delta T$ is the instantaneous temperature difference between the two sensors, and 1.231 is an empirically derived constant.

Abnormal *SFD* data due to instrument problems (less than 1% of the total records) were excluded from subsequent analysis. The remaining *SFD* values were used to calculate two *SFD* ratios that would let us evaluate the difference in drought stress effects between trees of different sizes. The first parameter, $Ratio_d$, represents the diurnal drought stress. This is the ratio of the mean *SFD* from 11:00 to 15:00 ('noon', subscript n) to the mean *SFD* for all data collected during the periods from 07:00 to 11:00 ('morning', subscript m) and from 15:00 to 19:00 ('afternoon', subscript a) for the same tree:

$$Ratio_{\mathrm{d}} = \frac{\sum_{i=1}^{N_n} SFD_{\mathrm{n}}(i)}{N_{\mathrm{n}}} \Bigg/ \frac{\sum_{i=1}^{N_{\mathrm{m\&a}}} SFD_{\mathrm{m\&a}}(i)}{N_{\mathrm{m\&a}}} \quad (7)$$

where $SFD_{\mathrm{n}}(i)$ is the mean *SFD* during the 'noon' period and $N_{\mathrm{n}}$ is the number of measurements during this period for individual $i$. Because the measurement interval was 30 min, $N_{\mathrm{n}} = 8$. $SFD_{\mathrm{m\&a}}(i)$ is the mean *SFD* for the morning and afternoon periods combined, and $N_{\mathrm{m\&a}}$ is the number of measurements during the morning and afternoon periods combined (=17).

The second parameter is $Ratio_{\mathrm{s}}$, which represents the seasonal drought stress and equals the ratio of the mean *SFD* during the dry season (from October to March, subscript 'd') to the mean *SFD* during the preceding wet season (April–September, subscript 'w') for the same tree:

$$Ratio_{\mathrm{s}} = \frac{\sum_{i=1}^{N_{\mathrm{d}}} SFD_{\mathrm{d}}(i)}{N_{\mathrm{d}}} \Bigg/ \frac{\sum_{i=1}^{N_w} SFD_{\mathrm{w}}(i)}{N_{\mathrm{w}}} \quad (8)$$

where $SFD_{\mathrm{d}}(i)$ represents the mean daytime *SFD* (07:00–19:00) during the dry season, and $N_{\mathrm{d}}$ (=13 175) is the number of measurements during this period. $SFD_{\mathrm{w}}(i)$ is the mean *SFD* during the wet season and $N_{\mathrm{w}}$ (=12 825) is the corresponding number of measurements.

### *Climatic variables*

A previous study at the same site (Zhou *et al.*, 2011) provides details of the long-term changes in air temperature, precipitation, the annual numbers of days with no rain or with light rain (<10 mm day$^{-1}$), and soil moisture. In this study, we used this climatic data to calculate Pearson's correlation coefficient between the climate parameters and the following tree parameters: living biomass, DBH growth rate, and tree mortality, and recruitment rates. We averaged the annual climatic variables across all years between consecutive surveys after 1978 and averaged the annual climatic variables between 1973 and 1978 for the survey in 1978 (Table 1).

### *Statistical analysis*

Prior to any statistical analysis, data must be tested to confirm normality, and to detect autocorrelation. Where data did not

**Table 1** Average climatic parameters during the various survey periods

| | AMT (°C) | HMT (°C) | CMT (°C) | DST (°C) | WST (°C) | AP (mm) | DSP (mm) | WSP (mm) | NRD (no.) | LRD (no.) | SWC (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1973–1978 | 21.9 | 28.6 | 13.0 | 17.1 | 26.7 | 1675 | 303 | 1372 | 205.2 | 112.6 | 145.0 |
| 1979–1982 | 22.3 | 29.0 | 15.2 | 17.9 | 26.6 | 1695 | 334 | 1361 | 211.3 | 102.8 | 137.5 |
| 1983–1992 | 22.4 | 29.1 | 13.8 | 17.6 | 27.0 | 1589 | 385 | 1204 | 209.5 | 108.4 | 133.7 |
| 1993–1994 | 22.5 | 29.0 | 13.7 | 17.9 | 27.0 | 1990 | 280 | 1710 | 198.0 | 111.0 | 120.8 |
| 1995–1999 | 22.7 | 28.8 | 14.4 | 18.3 | 27.0 | 1666 | 299 | 1367 | 211.6 | 104.4 | 121.5 |
| 2000–2004 | 22.7 | 28.6 | 14.5 | 18.2 | 27.1 | 1464 | 288 | 1176 | 221.6 | 98.4 | 109.1 |
| 2005–2008 | 22.7 | 29.3 | 14.0 | 18.4 | 27.0 | 1777 | 254 | 1523 | 223.3 | 92.5 | 103.9 |
| 2009–2010 | 22.9 | 29.2 | 12.8 | 18.5 | 27.3 | 1540 | 308 | 1232 | 230.0 | 90.0 | 97.0 |

Parameters

AMT, annual mean temperature; HMT, hottest month temperature; CMT, coldest month temperature; DST, dry season temperature; WST, wet season temperature; AP, annual precipitation; DSP, dry season precipitation; WSP, wet season precipitation; NRD, no-rain days; LRD, light-rain days; SWC, soil water content to a depth of 50 cm in the dry season.

meet the statistical assumptions for a given test, we transformed the data or used alternative statistical tests (i.e. a distribution-free nonparametric test). We used the least-squares method to obtain linear fits for trends in the age composition, in the living biomass (t $ha^{-1}$), in the stem density (individuals $ha^{-1}$), in the relative mortality and recruitment rates (% $yr^{-1}$), in diameter growth rates (mm $yr^{-1}$), and in the number of species with living stems. We also used the least-squares method to obtain linear correlations between the two *SFD* ratios and the tree's DBH. If the slopes of the regressions differed significantly from 0 (*t*-test, $P < 0.05$), we considered the trends to be statistically significant.

## Results

Since 1978, the annual numbers of rain-free days, annual mean temperature, and mean dry-season temperature have increased by about 23.7 ± 3.2 days, 0.6 ± 0.1 °C, and 0.8 ± 0.2 °C, respectively. The annual number of light-rain days (less than 10 mm $day^{-1}$) and soil water content in the dry season to a depth of 50 cm decreased by about 20.5 ± 2.1 days and 45.2 ± 6.3 mm, respectively (Zhou *et al*., 2011). During the same period, the total living biomass and the number of trees decreased and increased significantly, respectively. The dynamics of the trees in the study forest in different functional groups and age classes responded differently to climate change during this period.

### *Endogenous changes in DBH growth and age composition of the whole community*

Figure 1 shows changes in the *ADGR* driven by endogenous factors. *ADGR* increased when DBH was smaller than 20 cm and the age was in the 62–82 year age class or younger, reached a maximum at a DBH between 20 and 24 cm and an age range of 82–90 years, and then remained stable. Due to the highly complex species composition, the community as a whole showed a stable, long-term DBH growth rate after an age of 82 years. From Fig. 1, we calculated that the yearly *ADGR* increments were 0.014 mm $yr^{-2}$, 0.0057 mm $yr^{-2}$, 0.00087 mm $yr^{-2}$, and −0.00085 mm $yr^{-2}$ for DBH classes 1 cm ≤ DBH ≤ 5 cm, 5 cm < DBH ≤ 10 cm, 10 cm < DBH ≤ 20 cm, and DBH > 20 cm, respectively. These *ADGR* increments were taken to be the contribution of endogenous factors to DBH growth.

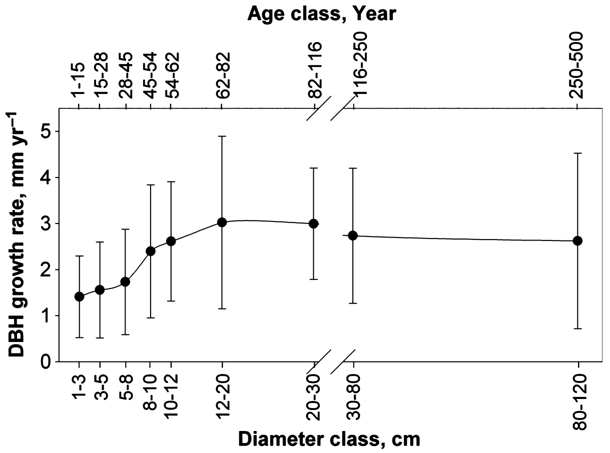

**Fig. 1** The relationship between the average DBH growth rate (*ADGR*) and DBH or the age of individuals.

Figure 2a shows the estimated age composition of the forest. From 1978 to 2010, the proportions of the individuals younger than 50 years (DBH ranges 1–10 cm), 50–100 years (DBH ranges 10–25 cm), and older than 100 years (DBH ranges >25 cm) amounted to 83.5–92.4%, 14.3–5.7%, and 2.5%, respectively. For these age classes, the proportions increased

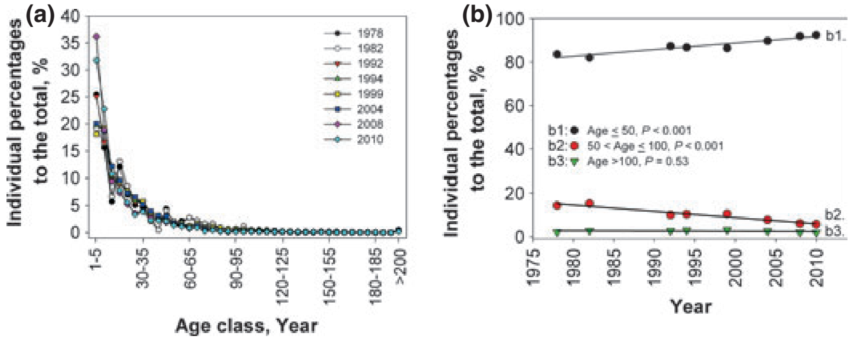

**Fig. 2** Age composition and temporal trends of different age groups. (a) Age composition and (b) temporal trends of different age groups.

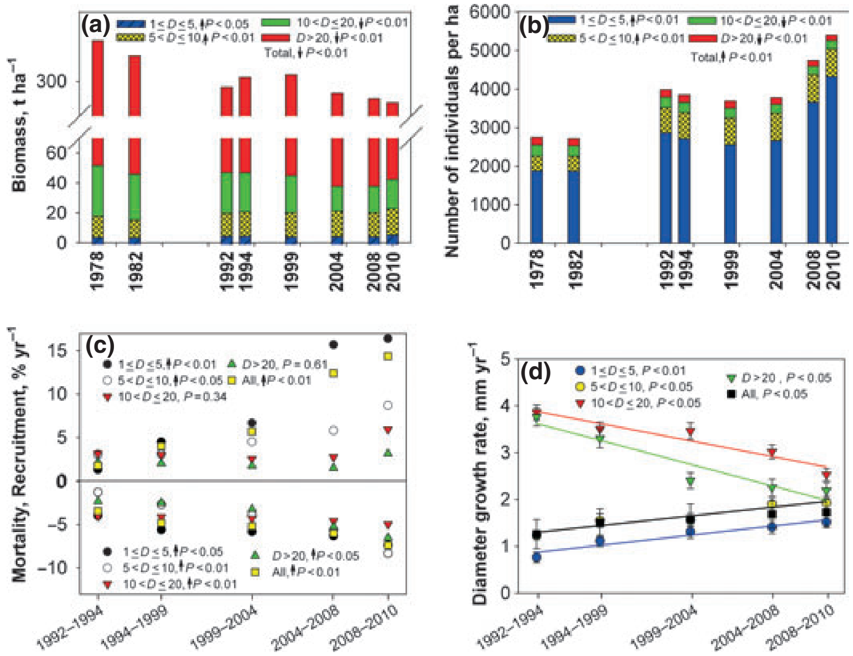

**Fig. 3** Changes in community parameters for individuals in the four DBH classes: (a) biomass; (b) number of individuals; (c) recruitment (above zero line), and mortality (below zero line) rates; (d) diameter growth rate. In (d), the slopes of the lines are 0.043, 0.041, −0.074, and −0.10 mm $yr^{-2}$ for 1 $\leq$ DBH $\leq$ 5 cm, 5 < DBH $\leq$ 10 cm, 10 < DBH $\leq$ 20 cm, and DBH > 20 cm, respectively. ↓, significant decrease; ↑, significant increase.

significantly, decreased significantly, and showed no significant change, respectively, during the study period (Fig. 2b). The monsoon evergreen broad-leaved forest has therefore been undergoing a transition from a community with a relatively stable age structure dominated by large individuals to a community with an increasing proportion of younger individuals. During this process, the most striking features are the significant decrease in middle-aged trees (50–100 years) and no change in the oldest trees (older than 100 years). A lasting decrease in the proportion of middle-aged individuals will eventually result in a decrease in the number of old individuals.

### *DBH Classes*

Both the living biomass and the number of individuals in the two largest DBH classes (DBH > 10 cm) decreased significantly from 1978 to 2010, whereas the biomass and number of individuals in the two smallest DBH classes (DBH $\leq$ 10 cm) increased significantly (Fig. 3a and b). The mortality rates increased significantly for individuals in all DBH classes (Fig. 3c). However, the recruitment rates showed different patterns in the four DBH classes, with significant increases in the average for all individuals combined and for individuals in the two smallest DBH classes, but there were no

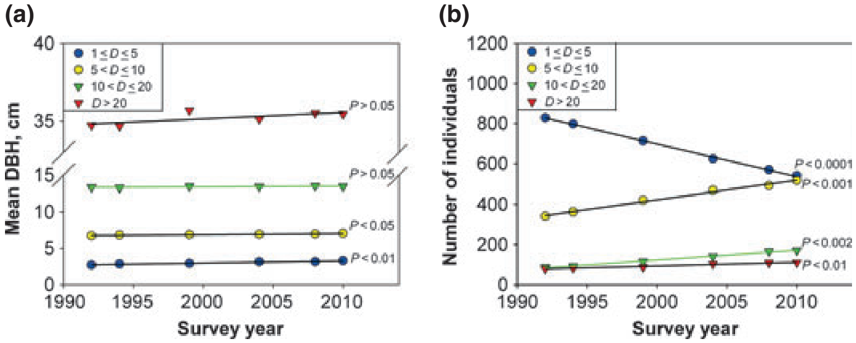

**Fig. 4** Trends for (a) mean DBH (*D*) and (b) dynamic changes in the number of individuals in the four DBH classes for the 1337 individuals that remained alive from 1992 to 2010.

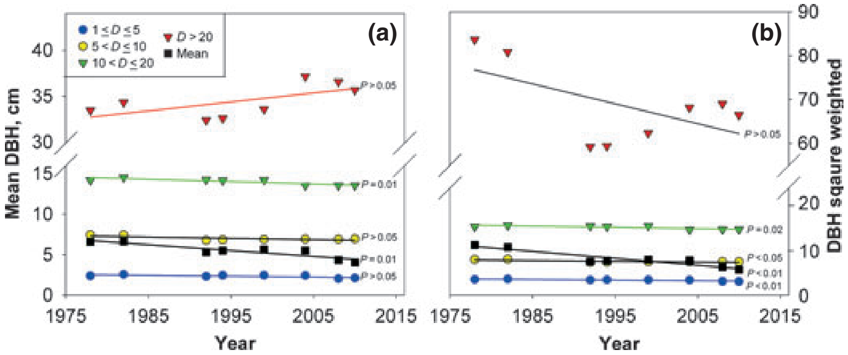

**Fig. 5** Trends in mean DBH (*D*) for individuals in the four DBH classes and for the community as a whole: (a) simple arithmetic average; (b) DBH square-weighted average.

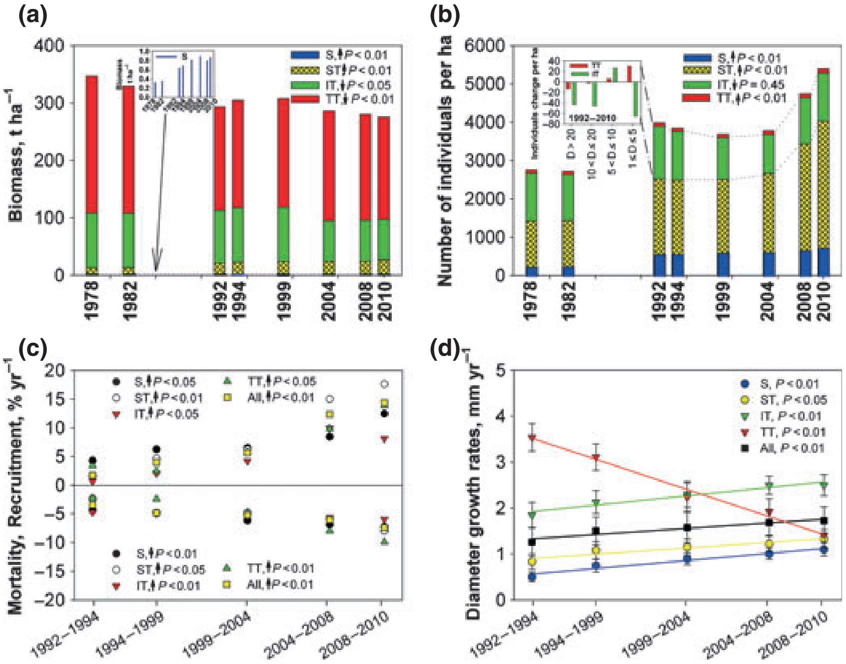

**Fig. 6** Changes in community parameters for the four functional groups: (a) biomass; (b) number of individuals; (c) recruitment (above zero line) and mortality (below zero line) rates; (d) diameter growth rate. ↓, significant decrease; ↑, significant increase. S, shrub; ST, short tree; IT, intermediate tree; TT, tall tree.

significant trends for individuals in the two largest DBH classes. For the 1337 trees that remained alive from 1992 to 2010, the mean diameter growth rates (DGR) for all individuals and for those in the two smallest DBH classes increased significantly, whereas those in the two largest DBH classes decreased significantly (Fig. 3d).

Here, we make an analysis to roughly estimate the contribution of exogenous factors to the changes of DGR. The slopes shown in Fig. 3d were 0.043, 0.041, −0.074, and −0.10 mm yr$^{-2}$ for $1 \leq$ DBH $\leq 5$ cm, $5 <$ DBH $\leq 10$ cm, $10 <$ DBH $\leq 20$ cm, and DBH $> 20$ cm, respectively. Correspondingly, the estimated yearly *ADGR* increments were 0.014, 0.0057, 0.00087, and −0.00085 mm yr$^{-2}$ for the same sequence of DBH classes as pointed out earlier when describing the result shown in Fig. 1. Combining the two results, we can find that the contributions of endogenous factors (e.g. age effects, represented by ADGR) to the changes of DBH growth rate were limited. In contrast, 67% of the slope in the 1 cm $\leq$ DBH $\leq$ 5 cm, 86% in the 5 cm $<$ DBH $\leq$ 10 cm, 101% in the 10 cm $<$ DBH $\leq$ 20 cm, and 99% in the DBH $>$ 20 cm were driven by exogenous factors.

Further analysis revealed that the average DBHs for the two largest DBH classes did not increase significantly from 1992 to 2010 (Fig. 4a) due to significant new recruitment in these DBH classes (i.e. recruitment of smaller individuals at the lower end of this class decreased the average value; Fig. 4b), suggesting that

**Table 2** Temporal trends in number of individuals in each DBH class and percentage of total number for every functional group from 1978 to 2010

| Functional group | DBH class | Percentage (F)/ Number (N) | 1978 | 1982 | 1992 | 1994 | 1999 | 2004 | 2008 | 2010 |
|---|---|---|---|---|---|---|---|---|---|---|
| Tall tree | $1 \leq$ DBH $\leq 5$ cm$^{**}$↑ | F | 19.9 | 21.4 | 23.0 | 23.9 | 34.0 | 35.0 | 45.5 | 48.7 |
| | | N | 16 | 17 | 20 | 22 | 31 | 33 | 46 | 53 |
| | $5 <$ DBH $\leq 10$ cm$^{*}$↑ | F | 8.6 | 8.3 | 8.0 | 9.0 | 9.4 | 12.8 | 13.9 | 14.5 |
| | | N | 7 | 7 | 7 | 8 | 8 | 12 | 14 | 16 |
| | $10 <$ DBH $\leq 20$ cm$^{*}$↓ | F | 9.4 | 8.4 | 8.0 | 7.2 | 5.6 | 4.8 | 4.6 | 4.7 |
| | | N | 8 | 7 | 7 | 6 | 5 | 5 | 5 | 5 |
| | DBH $> 20$ cm$^{***}$↓ | F | 62.1 | 61.9 | 61.0 | 59.9 | 51.0 | 47.4 | 36.0 | 32.1 |
| | | N | 50 | 51 | 54 | 54 | 46 | 44 | 36 | 35 |
| Intermediate tree | $1 \leq$ DBH $\leq 5$ cm | F | 59.3 | 60.0 | 63.2 | 59.5 | 56.8 | 59.8 | 65.1 | 68.7 |
| | | N | 748 | 729 | 880 | 763 | 627 | 618 | 788 | 868 |
| | $5 <$ DBH $\leq 10$ cm$^{*}$↑ | F | 10.9 | 10.8 | 12.4 | 14.7 | 14.9 | 15.7 | 14.8 | 14.1 |
| | | N | 138 | 131 | 172 | 188 | 164 | 162 | 179 | 178 |
| | $10 <$ DBH $\leq 20$ cm$^{**}$↓ | F | 17.9 | 18.2 | 14.8 | 15.5 | 16.2 | 12.7 | 11.6 | 9.8 |
| | | N | 226 | 221 | 206 | 199 | 179 | 131 | 140 | 124 |
| | DBH $> 20$ cm | F | 11.9 | 11.0 | 9.6 | 10.3 | 12.1 | 11.8 | 8.5 | 7.4 |
| | | N | 150 | 134 | 133 | 132 | 133 | 123 | 104 | 94 |
| Short tree | $1 \leq$ DBH $\leq 5$ cm | F | 74.7 | 74.5 | 72.1 | 71.2 | 68.5 | 68.7 | 78.4 | 81.2 |
| | | N | 863 | 862 | 1384 | 1349 | 1281 | 1383 | 2155 | 2662 |
| | $5 <$ DBH $\leq 10$ cm | F | 20.4 | 21.3 | 24.7 | 25.4 | 27.6 | 26.5 | 19.0 | 16.0 |
| | | N | 236 | 246 | 474 | 480 | 516 | 533 | 523 | 524 |
| | $10 <$ DBH $\leq 20$ cm | F | 4.9 | 4.1 | 3.0 | 3.2 | 3.6 | 4.6 | 2.4 | 2.6 |
| | | N | 57 | 48 | 58 | 61 | 67 | 93 | 66 | 85 |
| | DBH $> 20$ cm | F | 0.0 | 0.1 | 0.2 | 0.2 | 0.3 | 0.2 | 0.2 | 0.2 |
| | | N | 0 | 1 | 4 | 4 | 6 | 4 | 5 | 7 |
| Shrub | $1 \leq$ DBH $\leq 5$ cm | F | 98.9 | 98.8 | 98.9 | 99.0 | 98.9 | 98.5 | 99.3 | 99.0 |
| | | N | 248 | 257 | 576 | 575 | 616 | 624 | 669 | 736 |
| | $5 <$ DBH $\leq 10$ cm | F | 1.1 | 1.2 | 1.1 | 1.0 | 1.1 | 1.5 | 0.7 | 0.9 |
| | | N | 3 | 3 | 6 | 6 | 7 | 10 | 5 | 7 |
| | $10 <$ DBH $\leq 20$ cm | F | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 |
| | | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| | DBH $> 20$ cm | F | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**P* = 0.05–0.01; ***P* = 0.01–0.001; ****P* < 0.001.

↑, uptrend; ↓, downtrend; F, percentages of the number of individuals in each DBH class relative to the total number for the functional group; N, number of individuals in each DBH class.

**Table 3** Temporal trends in percentages of the total number of individuals in each functional group in each DBH class from 1978 to 2010

| | | Proportion of total number of individuals (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| DBH class | Functional group | 1978 | 1982 | 1992 | 1994 | 1999 | 2004 | 2008 | 2010 |
| $1 \leq$ DBH $\leq 5$ cm | Tall tree | 0.9 | 0.9 | 0.7 | 0.8 | 1.2 | 1.2 | 1.3 | 1.2 |
| | Intermediate tree$^{***}$↓ | 39.9 | 39.1 | 30.8 | 28.2 | 24.5 | 23.3 | 21.5 | 20.1 |
| | Short tree$^{**}$↑ | 46.0 | 46.2 | 48.4 | 49.8 | 50.2 | 52.0 | 58.9 | 61.6 |
| | Shrub | 13.2 | 13.8 | 20.1 | 21.2 | 24.1 | 23.5 | 18.3 | 17.1 |
| $5 <$ DBH $\leq 10$ cm | Tall tree | 1.8 | 1.8 | 1.1 | 1.2 | 1.2 | 1.7 | 1.9 | 2.2 |
| | Intermediate tree$^{**}$↓ | 35.9 | 33.9 | 26.1 | 27.6 | 23.6 | 22.6 | 24.9 | 24.6 |
| | Short tree$^{*}$↑ | 61.6 | 63.6 | 71.8 | 70.4 | 74.2 | 74.4 | 72.5 | 72.3 |
| | Shrub | 0.7 | 0.8 | 1.0 | 0.9 | 1.0 | 1.3 | 0.7 | 0.9 |
| $10 <$ DBH $\leq 20$ cm | Tall tree | 2.6 | 2.5 | 2.6 | 2.4 | 2.0 | 2.0 | 2.2 | 2.4 |
| | Intermediate tree$^{*}$↓ | 77.9 | 80.3 | 76.1 | 74.8 | 71.2 | 57.5 | 66.5 | 57.6 |
| | Short tree$^{*}$↑ | 19.5 | 17.2 | 21.3 | 22.8 | 26.8 | 40.5 | 31.3 | 39.6 |
| | Shrub | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 |
| DBH $> 20$ cm | Tall tree | 25.1 | 27.4 | 28.1 | 28.4 | 24.8 | 26.1 | 25.1 | 25.9 |
| | Intermediate tree | 74.9 | 72.0 | 69.9 | 69.6 | 72.2 | 71.5 | 71.1 | 69.2 |
| | Short tree$^{***}$↑ | 0.0 | 0.6 | 2.0 | 2.0 | 3.0 | 2.4 | 3.8 | 4.9 |
| | Shrub | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

*$P$ = 0.05–0.01; **$P$ = 0.01–0.001; ***$P$ < 0.001.
↑, uptrend; ↓, downtrend.

the significant decreases in mean diameter growth rates in these DBH classes were not caused by natural senescence.

Thus, the survival and growth of the two largest groups of individuals were restrained, whereas those of the two smallest groups of individuals improved due to differences in mortality and recruitment rates and differences in diameter growth rates among the DBH classes. As a result of the above-mentioned changes, the monsoon evergreen broad-leaved forest community has undergone a transition from a structure dominated by a cohort of fewer and larger individuals to a structure that is increasingly dominated by a cohort of more and smaller individuals. The mean DBH for all individuals combined in the plots decreased significantly during the study period, from ~ 6.6 cm (simple arithmetic average) and 11.2 cm (DBH$^2$-weighted average) in 1978– 4.1 and 5.7 cm, respectively, in 2010 (Fig. 5a and b). With the decreasing mean size of the individuals, the living biomass decreased significantly (Fig. 3a) and the number of individuals increased significantly (Fig. 3b).

### *Functional groups*

Figure 6a shows that the living biomass contributed by the tall and intermediate trees decreased significantly, whereas those of short trees and shrubs increased significantly. The number of living individuals increased significantly for tall trees, but did not change significantly for intermediate trees (Fig. 6b). In contrast, the number of living short trees and shrubs almost doubled (Fig. 6b). Figure 6c shows that both mortality and recruitment rates increased significantly for all four functional groups. For the 1337 individuals that remained alive from 1992 to 2010, the mean diameter growth rates of the intermediate trees, short trees, and shrubs increased significantly, whereas the mean diameter growth of tall trees decreased significantly (Fig. 6d).

Table 2 shows that both the percentage and the number of smaller individuals ($1 \leq$ DBH $\leq 10$ cm) in the tall trees group increased significantly, whereas both the percentage and the number of bigger individuals (DBH > 10 cm) decreased significantly from 1978 to 2010. For the intermediate trees, the percentage of individuals in the $5 <$ DBH $\leq 10$ cm size class increased significantly, whereas the number of individuals in the $10 <$ DBH $\leq 20$ DBH class decreased significantly. The numbers in the smallest and largest size classes increased and decreased, respectively, but the differences were not significant. There were no significant changes in any DBH class for the short trees and shrubs. Table 3 shows that the proportion of short trees in all four DBH classes increased significantly, whereas the proportion of intermediate trees decreased significantly in all DBH classes except the >20 cm class.

In summary, our analysis of the functional group results suggests that the monsoon evergreen broad-leaved forest is changing toward a community dominated by short trees and shrubs.

### *Changes in species composition*

The species composition also changed significantly during the study period. The number of living species increased significantly, with significant increases in both the number of recruited species and the number of disappeared species (Fig. 7). Although the species that were either recruited or disappeared were all rare species within the climax community, and their fluctuations had little influence on the total carbon pool or on the total number of individuals, these changes suggest that the species composition of the monsoon evergreen broad-leaved forest has become unstable, and this may jeopardize biodiversity conservation. The influence of species changes on the carbon pool and on the number of individuals resulted mostly from changes in the main species, which were those with many individuals or a large DBH (Table S1). The species with a significantly decreased number of living individuals from 1978 to 2010 accounted for 24.6% of the total living species, vs. 33.6% that showed a significant increase and 41.8% that showed no significant change (Table 4). These species accounted for 40.9%, 35.6%, and 23.6% of the total number of living individuals, and 61.9%, 19.4%, and 18.8% of the total living biomass (Table 4).

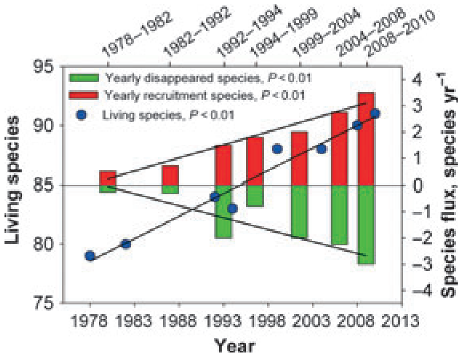

**Fig. 7** Changes in the number of living, recruited, and disappeared species from 1978 to 2010.

### *Regression analysis*

As Table 5 shows, the increasing number of days per year with no rain contributed significantly to the biomass trends in the $10 < \text{DBH} \leq 20$ cm class, to DBH growth rates in all DBH classes, to mortality rates in the classes with $1 \leq \text{DBH} \leq 20$ cm, and to recruitment rates in the classes with $1 \leq \text{DBH} \leq 10$ cm. The decreasing number of days per year with light rain contributed significantly to the biomass trend in the $10 < \text{DBH} \leq 20$ cm class and the total for all classes combined, to DBH growth rates in all classes, to mortality rates in all classes, and to recruitment rates in classes with $1 \leq \text{DBH} \leq 10$ cm. The rising annual mean temperature contributed significantly to the biomass trend in the classes with $\text{DBH} > 5$ cm and the total for all classes combined, to DBH growth rates in the class with $10 < \text{DBH} \leq 20$ cm, and to mortality rates in the classes with $1 \leq \text{DBH} \leq 20$ cm, but not to recruitment rates. The increasing dry-season mean temperature contributed significantly to the biomass trend in the classes with $\text{DBH} > 10$ cm and to the total for all

**Table 4** Trends for the number of individuals in each functional group and the associated percentages of the total number of species, average number of individuals, and total biomass from 1978 to 2010

| Functional group | Trends for the number of individuals in each functional group from 1978 to 2010 | Percentage of total number of species (%) | Percentage of average number of individuals (%) | Percentage of the average biomass (%) |
|---|---|---|---|---|
| Tall tree | Significant decrease ($P < 0.05$) | 1.82 | 1.08 | 54.36 |
| | Significant increase ($P < 0.05$) | 1.82 | 0.89 | 2.62 |
| | No significant trend ($P > 0.05$) | 3.64 | 0.17 | 5.98 |
| Intermediate tree | Significant decrease ($P < 0.05$) | 10.00 | 9.94 | 2.45 |
| | Significant increase ($P < 0.05$) | 12.73 | 9.01 | 12.54 |
| | No significant trend ($P > 0.05$) | 13.64 | 9.11 | 12.28 |
| Short tree | Significant decrease ($P < 0.05$) | 9.09 | 25.04 | 4.88 |
| | Significant increase ($P < 0.05$) | 14.55 | 25.34 | 4.20 |
| | No significant trend ($P > 0.05$) | 13.64 | 3.36 | 0.39 |
| Shrub | Significant decrease ($P < 0.05$) | 3.64 | 4.81 | 0.18 |
| | Significant increase ($P < 0.05$) | 4.55 | 0.32 | 0.00 |
| | No significant trend ($P > 0.05$) | 10.91 | 10.93 | 0.13 |
| Total | Significant decrease ($P < 0.05$) | 24.55 | 40.87 | 61.87 |
| | Significant increase ($P < 0.05$) | 33.64 | 35.57 | 19.37 |
| | No significant trend ($P > 0.05$) | 41.82 | 23.56 | 18.76 |

**Table 5** Pearson's correlation coefficients between the five climatic variables and the living biomass, DBH growth rate, mortality rate, and recruitment rate in each of the DBH classes and for all classes combined

| | | Climatic variables | | | | |
|---|---|---|---|---|---|---|
| | | Annual no-rain days | Annual light-rain days | Annual mean temperature (°C) | Mean dry-season temperature (°C) | Soil water content (mm) to a depth of 50 cm in the dry season |
| Living biomass ($n$ = 8) | | | | | | |
| Total | Slope | −1.60 | 2.16 | −72.1 | −40.9 | 1.29 |
| | $R^2$ | 0.46 | 0.54 | 0.77 | 0.59 | 0.79 |
| | $P$ | ~ | * | ** | * | ** |
| DBH > 20 cm | Slope | −1.25 | 1.69 | −59.9 | −32.7 | 1.05 |
| | $R^2$ | 0.39 | 0.45 | 0.73 | 0.52 | 0.72 |
| | $P$ | ~ | ~ | ** | * | ** |
| 10 < DBH ≤ 20 cm | Slope | −0.45 | 0.60 | −18.1 | −11.0 | 0.34 |
| | $R^2$ | 0.57 | 0.64 | 0.75 | 0.67 | 0.88 |
| | $P$ | * | * | ** | * | *** |
| 5 < DBH ≤ 10 cm | Slope | 0.08 | −0.10 | 4.67 | 2.30 | −0.09 |
| | $R^2$ | 0.21 | 0.19 | 0.56 | 0.32 | 0.46 |
| | $P$ | ~ | ~ | * | ~ | ~ |
| 1 ≤ DBH ≤ 5 cm | Slope | 0.02 | −0.03 | 1.18 | 0.53 | −0.02 |
| | $R^2$ | 0.19 | 0.19 | 0.43 | 0.21 | 0.47 |
| | $P$ | ~ | ~ | ~ | ~ | ~ |
| DBH growth rate ($n$ = 5) | | | | | | |
| DBH < 20 cm | Slope | −0.06 | 0.08 | −3.64 | −2.58 | 0.06 |
| | $R^2$ | 0.94 | 0.93 | 0.55 | 0.58 | 0.85 |
| | $P$ | ** | ** | ~ | ~ | * |
| 10 < DBH ≤ 20 cm | Slope | −0.04 | 0.06 | −3.34 | −2.18 | 0.04 |
| | $R^2$ | 0.80 | 0.88 | 0.88 | 0.79 | 0.84 |
| | $P$ | * | * | * | * | * |
| 5 < DBH ≤ 10 cm | Slope | 0.02 | −0.03 | 1.67 | 1.24 | −0.02 |
| | $R^2$ | 0.86 | 0.95 | 0.72 | 0.84 | 0.80 |
| | $P$ | * | ** | ~ | * | * |
| 1 ≤ DBH ≤ 5 cm | Slope | 0.02 | −0.03 | 1.78 | 1.28 | −0.02 |
| | $R^2$ | 0.99 | 0.96 | 0.74 | 0.81 | 0.79 |
| | $P$ | *** | ** | ~ | * | * |
| Mortality rate ($n$ = 5) | | | | | | |
| DBH < 20 cm | Slope | 0.12 | −0.20 | 10.8 | 6.77 | −0.16 |
| | $R^2$ | 0.70 | 0.85 | 0.70 | 0.59 | 0.91 |
| | $P$ | ~ | * | ~ | ~ | * |
| 10 < DBH ≤ 20 cm | Slope | 0.03 | −0.04 | 2.32 | 1.43 | −0.03 |
| | $R^2$ | 0.78 | 0.87 | 0.80 | 0.64 | 0.94 |
| | $P$ | * | * | * | ~ | ** |
| 5 < DBH ≤ 10 cm | Slope | 0.20 | −0.30 | 17.6 | 11.2 | −0.25 |
| | $R^2$ | 0.84 | 0.91 | 0.86 | 0.74 | 0.91 |
| | $P$ | * | * | * | ~ | * |
| 1 ≤ DBH ≤ 5 cm | Slope | 0.10 | −0.14 | 8.19 | 5.67 | −0.10 |
| | $R^2$ | 0.94 | 0.90 | 0.91 | 0.93 | 0.85 |
| | $P$ | ** | * | * | ** | * |
| Recruitment rates ($n$ = 5) | | | | | | |
| DBH < 20 cm | Slope | 0.01 | −0.02 | 2.85 | 1.13 | −0.02 |
| | $R^2$ | 0.06 | 0.06 | 0.43 | 0.14 | 0.14 |
| | $P$ | ~ | ~ | ~ | ~ | ~ |
| 10 < DBH ≤ 20 cm | Slope | 0.05 | −0.08 | 7.67 | 3.67 | −0.08 |

**Table 5** (continued)

| | | Climatic variables | | | | |
|---|---|---|---|---|---|---|
| | | Annual no-rain days | Annual light-rain days | Annual mean temperature (°C) | Mean dry-season temperature (°C) | Soil water content (mm) to a depth of 50 cm in the dry season |
| | $R^2$ | 0.21 | 0.23 | 0.62 | 0.30 | 0.35 |
| | $P$ | ~ | ~ | ~ | ~ | ~ |
| 5 < DBH ≤ 10 cm | Slope | 0.16 | −0.24 | 14.5 | 8.44 | −0.21 |
| | $R^2$ | 0.81 | 0.79 | 0.74 | 0.57 | 0.73 |
| | $P$ | * | * | ~ | ~ | ~ |
| 1 ≤ DBH ≤ 5 cm | Slope | 0.48 | −0.76 | 37.6 | 26.4 | −0.59 |
| | $R^2$ | 0.78 | 0.93 | 0.64 | 0.66 | 0.74 |
| | $P$ | * | ** | ~ | ~ | ~ |

~$P > 0.05$; *$P = 0.05$–$0.01$; **$P = 0.01$–$0.001$; ***$P < 0.001$.

classes combined, to DBH growth rates in the class with DBH ≤ 20 cm, and to mortality rates in the classes with 1 ≤ DBH ≤ 5 cm, but not to recruitment rates. The decline of soil water content during the dry season contributed significantly to the biomass trend in the classes with DBH > 10 cm and for all classes combined, to DBH growth rates in all classes, and to mortality rates in all classes, but not to recruitment rates. All five climatic variables therefore contributed to the observed vegetation shifts, especially for the decreasing soil water content during the dry season and the annual number of days with light rain, which are dominant factors that directly affect tree growth and survival.

### *Sap flow*

Sap flow measurements at our study sites from 2008 to 2011 showed that the ratio of sap flow during the period around noon (11:00–15:00) to sap flow during the rest of the daylight hours (07:00–11:00 and 15:00–19:00) decreased significantly with increasing tree DBH (Fig. 8a), and the same trend was observed for the ratio of sap flow in the dry season to sap flow in the wet season (Fig. 8b).

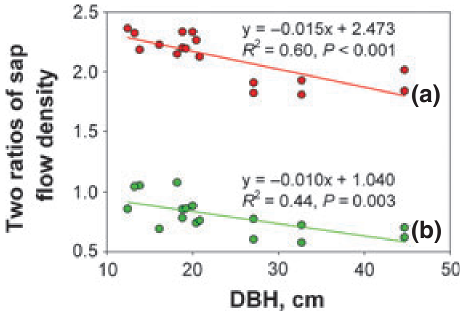

**Fig. 8** Changes in the sap flow ratio as a function of DBH for (a) the ratio of mean sap flow from 11:00 to 15:00 to sap flow during the rest of the daylight hours (07:00–11:00 and 15:00–19:00); (b) the ratio of mean sap flow during the dry season to mean sap flow during the wet season.

## Discussion

### *A comparison with other similar studies*

Based on long-term forest monitoring plots, several recent studies reported that climate change increased tree mortality in temperate (van Mantgem & Stephenson, 2007; van Mantgem *et al.*, 2009) and boreal forests (Peng *et al.*, 2011) or both mortality and recruitment rates in tropical forests (Lewis *et al.*, 2004a; Phillips *et al.*, 2004). As an important supplement in subtropical forests, our findings showed an imbalance in mortality and recruitment, and changes in diameter growth rates between larger and smaller trees and among different functional groups, which resulted in that the monsoon evergreen broad-leaved forest community was undergoing a transition from a forest dominated by a cohort of fewer and larger individuals to a forest dominated by a cohort of more and smaller individuals in the past more than three decades. The imbalance between big and small individuals was due to the difference in sensitivities to warming and drying environment between big and small individuals, which is exactly consistent to the result of drought experiment in an Amazon forest (Nepstad *et al.*, 2007).

The sap flow measurements for intermediate and tall trees have two important implications. First, they suggest that bigger individuals are more sensitive to drought stress than smaller individuals (Condit *et al.*, 2004; Nepstad *et al*., 2007), which may explain the differences in mortality and recruitment rates that we observed, why diameter growth rates differed between the bigger and smaller DBH classes, and why the mean DBH of all individuals in the monsoon evergreen broad-leaved forest decreased over time, similar to that reported by Sheridan & Bickford (2011) in other biomes. Second, the similarities between the two curves of sap flow ratios in Fig. 8 indicate that trees and shrubs in the Dinghushan Biosphere Reserve are water-restricted during the dry season because plants usually sustain more severe water stress around noon than they do at other times of day, and show more severe water stress during the dry season than during the wet season. In both cases, the degree of stress is greatest for the largest trees.

### *Connections with global warming and soil dryness*

Our previous report showed how the climatic variables in the subtropical regional forest responded to the warming that has occurred from 1978 to 2010 and the resulting drought stress (Zhou *et al*., 2011). Here, we performed regression analysis to identify the trends for the living biomass, DBH growth rate, and mortality and recruitment rates as functions of five climatic variables: the number of days with no rain, the number of days with light rain, the annual mean temperature, the mean dry-season temperature, and the soil water content to a depth of 50 cm (Table 5). The correlations provide direct evidence that rising temperatures and increasingly severe periods of drought contributed to the observed vegetation shifts in the past decades.

The article provides evidence that can potentially explain the observed shift since 1978 in the number of individuals of each species and in the community structure of the monsoon evergreen broad-leaved forest as a result of decreasing mean DBH in response to climate change. We believe that this shift has been caused by changes in environmental factors, including rising temperatures, more extreme precipitation patterns, increasing numbers of rain-free days, decreasing numbers of days with light rain, and increased soil drying (Zhou *et al*., 2011). Our regression analysis demonstrated significant connections between these changing climatic variables and the key growth and survival parameters that we analyzed for the monsoon evergreen broad-leaved forest. Our sap flow data provide additional evidence that the rising temperatures and increasingly severe periods of drought have decreased the survival of individuals with larger DBH and height. Although climatic change and the consequent increased frequency of soil drying may also affect the growth of smaller individuals, the more abundant sunlight due to an increasing number of rain-free days, a decreased number of days with light rain, and increased mortality of larger individuals is likely to improve the growth conditions for smaller individuals under a forest canopy (Condit *et al*., 2004).

Overall, the causal factors we have discussed may generate diameter growth rates, recruitment rates, and mortality rates that are unbalanced among the different DBH classes and functional groups, and this, in turn, may alter the community structure and drive the current climax community toward a community that is increasingly dominated by smaller individuals and by more species of short trees and shrubs. These alterations would affect the terrestrial ecosystem services provided by the monsoon evergreen broad-leaved forest, such as carbon sequestration and biodiversity conservation.

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## References

Allen CD, Breshears DD. (1998) Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences USA*, **95**, 14839–14842.

Breshears DD, Cobb NS, Rich PM *et al*. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences USA* **102**, 15144–15148.

Breshears DD, Myers OB, Meyer CW *et al*. (2009) Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*, **7**, 185–189.

Buol SW, Southard RJ, Graham RC, McDaniel PA (2003) *Soil Genesis and Classification* (5th edn), pp. 339–347. Iowa State Press, Iowa, USA.

Ciais P, Reichstein M, Viovy N *et al*. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences USA*, **100**, 5852–5857.

Clark DB, Clark DA, Oberbauer SF (2010) Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO2. *Global Change Biology*, **16**, 747–759.

Condit R, Aguilar S, Hernandez A *et al*. (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology*, **20**, 51–72.

da Costa ACL, Galbraith D, Almeida S *et al*. (2010) Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, **187**, 579–591.

Davidson EA, de Araújo AC, Artaxo P *et al*. (2012) The Amazon basin in transition. *Nature*, **481**, 321–328.

Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.

Enquist BJ, Enquist CAF (2011) Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. *Global Change Biology*, **17**, 1408–1424.

Feeley KJ, Wright SJ, Supardi MNN, Kassim AR, Davies SJ (2007) Decelerating growth in tropical forest trees. *Ecology Letters*, **10**, 461–469.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics*, **35**, 557–581.

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*, **3**, 309–320.

Institute of Botany, Chinese Academy of Sciences. (2005) Flora of China (Flora Reipublicae Popularis Sinicae) (online). Available at: http://frps.plantphoto.cn/pdf.asp.

IPCC (2007) *Climate Change (2007): The Physical Science Basis*. Cambridge Univ Press, New York.

Lewis SL, Phillips OL, Baker TR *et al.* (2004a) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society London Ser. B*, **359**, 421–436.

Lewis SL, Phillips OL, Sheil D *et al.* (2004b) Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. *Journal of Ecology*, **92**, 929–944.

Luo Y, Liu S, Fu SL, Liu JS, Wang GQ, Zhou GY (2008) Trends of precipitation in Beijiang River basin, Guangdong Province, China. *Hydrology Processes*, **22**, 2377–2386.

Ma ZH, Peng CH, Zhu QA *et al.* (2012) Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences USA*, **109**, 2423–2427.

Malhi Y, Aragao LEOC, Galbraith D *et al.* (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences USA*, **106**, 20610–20615.

van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters*, **10**, 909–916.

van Mantgem PJ, Stephenson NL, Byrne JC *et al.* (2009) Widespread Increase of Tree Mortality Rates in the Western United States. *Science*, **323**, 521–524.

McDowell N, Pockman WT, Allen CD *et al.* (2008) Mechanisms of plant survival and mortality during drought. Why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.

Mo JM, Zhang W, Zhu WX, Gundersen P, Fang YT, Li DJ, Wang H (2008) Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. *Global Change Biology*, **14**, 403–412.

Mueller RC, Scudder CM, Porter ME, Trotter RT III, Gehring CA, Whitham TG (2005) Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology*, **93**, 1085–1093.

Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology*, **88**, 2259–2269.

Peng CH, Ma ZH, Lei XD *et al.* (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature climate change*, **1**, 467–471.

Phillips OL, Baker TR, Arroyo L *et al.* (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society London Ser. B*, **359**, 381–407.

Phillips OL, Aragão LEOC, Lewis SL *et al.* (2009) Drought Sensitivity of the Amazon Rainforest. *Science*, **323**, 1344–1347.

Scheffer M, Bascompte J, Brock WA *et al.* (2009) Early-warning signals for critical transitions. *Nature*, **461**, 53–59.

Shen CD, Liu DS, Peng SL *et al.* (1999) $^{14}$C measurement of forest soils in Dinghushan Biosphere Reserve. *Chinese Science Bulletin*, **44**, 251–256.

Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. *Nature climate change*, **1**, 401–406.

Steppe K, De Pauw DJW, Doody TM, Teskey RO (2010) A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. *Agricultural and Forest Meteorology*, **150**, 1046–1056.

Tang XL, Liu SG, Zhou GY, Zhang DQ, Zhou CY (2006) Soil-atmospheric exchange of $CO_2$, $CH_4$, and $N_2O$ in three subtropical forest ecosystems in southern China. *Global Change Biology*, **12**, 546–560.

Tang XL, Wang YP, Zhou GY, Zhang DQ, Liu S (2011) Different patterns of ecosystem carbon accumulation between a young and an old-growth subtropical forest in Southern China. *Plant Ecology*, **212**, 1385–1395.

Walker B, Holling CS, Carpenter SR, Kinzig A (2004) Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society*, **9**, 5.

Wang BS, Ma MJ (1982) The successions of the Forest community in Dinghushan. *Tropical and Subtropical Forest Ecosystem Research*, **1**, 142–156. (in Chinese with English abstract).

Wen DZ, Wei P, Kong GH, Zhang QM, Huang ZL (1997) Biomass study of the community of Castanopsis chinensis, Schima superba, Cryptocarya concinna in a Southern China Reserve. *Acta Ecologica Sinica*, **17**, 497–504. (in Chinese with English abstract).

Willis KJ, Bailey RM, Bhagwat SA, Birks HJB (2010) Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution*, **25**, 583–591.

Yan JH, Wang YP, Zhou GY, Zhang DQ (2006) Estimates of soil respiration and net primary production of three forests at different succession stages in South China. *Global Change Biology*, **12**, 810–821.

Zhou GY, Liu SG, Li ZA *et al.* (2006a) Old-growth forests can accumulate carbon in soils. *Science*, **314**, 1417.

Zhou GY, Zhou CY, Liu SG *et al.* (2006b) Belowground carbon balance and carbon accumulation rate in the successional series of monsoon evergreen broad-leaved forest. *Science in China Series. D-Earth Sciences*, **49**, 311–321.

Zhou GY, Guan LL, Wei XH *et al.* (2007) Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in guangdong, China. *Plant Ecology*, **188**, 77–89.

Zhou GY, Wei XH, Luo Y *et al.* (2010) Forest recovery and river discharge at the regional scale of guangdong province, China. *Water Resources Research*, **46**, doi: 10.1029/2009WR008829.

Zhou GY, Wei XH, Wu YP *et al.* (2011) Quantifying the hydrological responses to climate change in an intact forested small watershed in Southern China. *Global Change Biology*, **17**, 3736–3746.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1** Species status in the community, including the plant functional group, the mean number of individuals, mean percentage of stand biomass, and trends in the number of individuals of each species during the study period (1978 to 2010).