

## LETTER

# Are functional traits a good predictor of global change impacts on tree species abundance dynamics in a subtropical forest?

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### Abstract

Significant changes in the composition of tree species have been observed in various forests worldwide. We hypothesised that these changes might result from variable sensitivities of species to global change, and species sensitivities might be quantified, using functional traits. Employing long-term (1978–2010) species abundance data of 48 tree species from a permanent subtropical forest plot, where multiple global change factors have been observed, including soil drying, we examined the relationships between temporal trends in abundance and suits of functional traits. We found that species with high photosynthesis rates, leaf phosphorus and nitrogen concentrations, specific leaf area, hydraulic conductivity, turgor loss point and predawn leaf water potential had increased in abundance, while species with opposite trait patterns had decreased. Our results demonstrate that functional traits underlie tree species abundance dynamics in response to drought stress, thus linking traits to compositional shifts in this subtropical forest under global changes.

### Keywords

Cavitation, drought stress, hydraulic conductivity, photosynthesis, plant economics, turgor loss point, xylem vulnerability.

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## INTRODUCTION

In recent decades, global climate changes (such as rising atmospheric CO<sub>2</sub> concentration, climate warming, and altered rainfall) have impacted vegetation worldwide (Lewis *et al.* 2009; Fauset *et al.* 2012; Soudzilovskaia *et al.* 2013). From the Arctic tundra to tropical rainforests, changes in the phenology, distribution, diversity, and community structure of plants have been widely observed (Parmesan 2006; Allen *et al.* 2010; Zhou *et al.* 2014). For instance, rising atmospheric CO<sub>2</sub> concentration, decreasing cloud cover and increasing solar radiation may ease several critical constraints to plant growth, leading to an increase in net primary production at a global scale (Nemani *et al.* 2003). At regional scales, it has been shown that global change-related environmental variability could potentially influence temporal changes in species composition, demographic rates, and biomass (Barber *et al.* 2000; Lewis *et al.* 2004; Phillips *et al.* 2004; van Mantgem *et al.* 2009; Feeley *et al.* 2011; Luo & Chen 2013; Brienen *et al.* 2015). Despite these well documented changes, forecasting the future impacts of global change on vegetation continues to present a formidable challenge (Van Bodegom *et al.* 2012).

A critical step towards accurately predicting climate change impacts on vegetation involves understanding how the

performance of a particular species is influenced by climate variables such as temperature and rainfall, as well as by its interaction with other species. Estimating these relationships requires long-term data, obtained under conditions where other anthropogenic factors such as land use change have a minimal impact. Measuring the responses of plant species to climate changes, using functional traits constitutes an improvement over traditional analyses, since functional traits of a plant species directly affect its performance under environmental change, and thus might increase our ability to understand global change drivers influencing species abundances (Van Bodegom *et al.* 2012; Mouillot *et al.* 2013). Soudzilovskaia *et al.* (2013) recently investigated whether plant functional traits can be used to predict changes in herbaceous species abundance in response to variations in temperature. Using long-term species abundance and functional trait data from meadow communities in the species-rich alpine belt of the Caucasus Mountains, they found that the observed responses of species abundance to different temperatures could be well predicted using a few functional traits. The authors further concluded that species with high resource investment into structural traits (e.g. thick leaves and low specific leaf area) and high quality seed production are better adapted to climate warming. Their approach provides

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a simple yet powerful method to predict future changes in species abundance, using a few readily measurable plant functional attributes.

The present study was conducted in a species-rich subtropical evergreen forest in southern China, where significant changes in species abundance have been observed over a 32-year period (from 1978 to 2010), and these changes have been attributed to climate change-induced soil drying (indicated by the decline of soil water content), which might result from global warming and enhanced rainfall seasonality with increases in the number of rain-free days, particularly during the dry seasons (Zhou *et al.* 2013). To explore potential drivers underlying the observed changes in species abundance of this forest community, we used an extensive data set on suites of functional traits to assess whether the observed changes in species abundance are related to their differences in functional traits. Specifically, we used a long-term (1978–2010) data set on the abundances (measured as total basal area, that is, the sum of the cross-sectional areas at breast-height of all individuals for each study species) of 48 dominant tree species, which account for 92% of the individuals in this subtropical forest community (Appendix S1 in the Supporting Information), and quantified a number of key functional traits that are direct measures of species resource acquisition strategies (leaf nitrogen and phosphorous concentrations, CO<sub>2</sub> assimilation rates, stomatal conductance, and stem hydraulic conductivity), as well as the ability of trees to cope with drought stress (xylem resistant to cavitation, stem hydraulic safety margin, predawn leaf water potential and leaf turgor loss point). Our hypothesis was that the changes in species abundance over time are a result of the difference in their functional traits, which allowed individual species to perform differently in resource acquisition and/or drought tolerance under global change.

## MATERIALS AND METHODS

### Study site, climatic parameters, and community surveys

The study site comprised an 1-ha permanent forest plot, located in the Dinghushan Biosphere Reserve (23°09'21" N–23°11'30" N, 112°32'39" E–112°35'41" E), about 84 km west of Guangzhou city, southern China. The region has a typical southern subtropical monsoon climate with annual average precipitation of 1678 mm, about 80% of which falls in the wet season from April to September, resulting in distinct seasonality of precipitation (Zhou *et al.* 2011). In 1978, an 8-ha experimental site was established in the core area of the reserve, with the 1-ha permanent forest plot towards the centre of the site. The plant community was characterised as a species-rich old-growth subtropical lowland evergreen forest, which has not been disturbed for more than 400 years, as evidently shown in a <sup>14</sup>C dating study on the forest soil (Shen *et al.* 1999), and a study on the successions of the forest community in Dinghushan (Wang & Ma 1982). In total, eight community surveys were performed in this permanent plot in 1978, 1982, 1992, 1994, 1999, 2004, 2008, and 2010, respectively. All living stems ≥ 1 cm in diameter at breast height (DBH) were identified and labeled. During the course of long-term monitoring, no noticeable disturbance events were

observed, for example, charcoal in soils and tree stumps with fire scars have not been found since the first survey in 1978 (Zhou *et al.* 2013). We used total basal area (BA) of each individual tree species to quantify its change in abundance over time, and BA was calculated as the sum of the cross-sectional areas at breast-height of all individuals for that species (Potvin & Gotelli 2008).

### Measurements of functional traits

We selected 12 functional traits to represent the major axes of tree functional variations. For each species, three to five individuals with DBH comparable to the mean DBH value of that species were sampled (Appendix S2). Traits of 19 out of the 48 study species were collected in an earlier work by Zhu *et al.* (2013), the rest were measured in this study.

We quantified the carbon, phosphorus and nitrogen economy of leaves by measuring specific leaf area (SLA), phosphorus concentration per leaf unit mass ( $P_{mass}$ ), and nitrogen concentration per leaf unit mass ( $N_{mass}$ ), which can be considered as part of the leaf economics spectrum (Reich *et al.* 1997; Wright *et al.* 2004a). For leaf area measurements, 20 fully expanded sun-exposed leaves in the canopy of three to five individuals per species were measured with a leaf area meter (Li-3000A; Li-Cor, Lincoln, NE, USA), with petioles and/or rachis removed. For shade-tolerant species grown in the understory, their leaves were collected from the top portion of the canopy. Leaves were oven-dried at 70 °C for 48 h to determine dry mass. SLA (cm<sup>2</sup> g<sup>-1</sup>) was calculated as leaf area per dry mass. The oven-dried leaves were then ground to fine powder.  $N_{mass}$  (mg g<sup>-1</sup>) was determined by Kjeldahl analysis, and  $P_{mass}$  (mg g<sup>-1</sup>) was measured using atomic absorption spectrophotometry.

We quantified light-capturing strategies via maximum CO<sub>2</sub> assimilation rate per unit mass ( $A_{mass}$ ; nmol g<sup>-1</sup> s<sup>-1</sup>) and stomatal conductance per unit mass ( $g_s$ ; mmol g<sup>-1</sup> s<sup>-1</sup>). Measurements of maximum CO<sub>2</sub> assimilation rate per unit area ( $A_{area}$ ; μmol m<sup>-2</sup> s<sup>-1</sup>) and stomatal conductance per unit area ( $g_{sa}$ ; mol m<sup>-2</sup> s<sup>-1</sup>) were conducted between 9 : 00 and 11 : 00 am on sunny days with a Li-6400 portable photosynthesis system (Li-6400, Li-Cor). Based on preliminary trials, the photosynthetic photon flux density was set at 1500 μmol m<sup>-2</sup> s<sup>-1</sup> to ensure that light-saturated photosynthetic rates were reached for all species. Ambient CO<sub>2</sub> and air temperature were maintained at 390 μmol mol<sup>-1</sup> and 28 °C respectively. Prior to the data being recorded, leaves were exposed to the above conditions for 5–10 min to allow for photosynthetic parameter stabilisation. For each species, five to ten fully expanded sun-exposed leaves were measured.  $A_{mass}$  was calculated as SLA ×  $A_{area}$ /10, and  $g_s$  was calculated as SLA ×  $g_{sa}$ /10.

We measured traits that relate to branch hydraulic conductivity via sapwood density (WD) and sapwood-specific hydraulic conductivity ( $K_S$ ). In brief, five to ten healthy and leaf-bearing branches (6–8 mm in diameter, 40–60 cm long) from three to five individuals per species were cut in the early morning, sealed in black plastic bags with moist towels, and immediately transported to the laboratory. Prior to measurements, branch samples were re-cut under water, with the cut ends being trimmed with a razor blade. To remove air embol-

lisms, branch segments were perfused with a filtered ( $\text{\O}$  0.2  $\mu\text{m}$ ) 20 mmol KCl solution at a pressure of 0.1 MPa for 20 min. Each segment was then connected to a hydraulic conductivity-measurement apparatus, following Sperry *et al.* (1988). An elevated water reservoir supplied the same perfusion solution to the segment, with a head pressure of  $\sim 6$  kPa. Water flow through the segment was allowed to equilibrate for  $\sim 10$  min, after which the mass of water flux through the segment over time (in seconds) was measured. The maximum hydraulic conductivity of the segment ( $K_h$ ) was calculated as  $K_h = FL/\Delta P$ , where  $F$  is the flow rate ( $\text{kg s}^{-1}$ ),  $\Delta P$  is the pressure gradient (MPa) through the segment, and  $L$  is the length of the segment (m). For sapwood area ( $A_s$ ), stem diameter (without bark) and pith diameter were measured, and the sapwood area was calculated as stem area subtract the pith area.  $K_S$  ( $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) is equivalent to  $K_h$  divided by the mean value of the sapwood cross-sectional area of both ends of the branch segment. Leaf area ( $A_l$ ) of all the leaves distal to the branch was measured with a leaf area meter (Li-3000A; Li-Cor). The higher the  $A_l/A_s$  ratio, the greater amount of leaf area per unit area of sapwood were able to carry. WD ( $\text{g cm}^{-3}$ ) was determined from the same branch segments as used for the hydraulic conductivity measurements. The volume of fresh sapwood (with bark and pith removed) was determined by the water displacement method (Poorter *et al.* 2010), and its dry mass was subsequently determined after oven-drying at 70 °C for 72 h. Then WD was calculated as the ratio of dry mass to fresh volume.

We also quantified stem drought tolerance by measuring xylem tension causing 50% loss of the  $K_S$  ( $\psi_{50}$ ). To measure xylem vulnerability to cavitation, we used the air-injection method to determine xylem vulnerability curves (Cochard *et al.* 1992). Branch segments ( $\sim 40$ – $60$  cm in length) were introduced into a pressure chamber (PMS, Corvallis, OR, USA) with both ends protruding. Proximal ends were connected to the hydraulic measuring equipment, and the maximum conductivity was measured. Subsequently, the pressure in the chamber was increased to 0.5 MPa and maintained for 10 min, and then lowered to 0.01 MPa and held for 20 min (to allow system equilibration), after which the branch hydraulic conductivity was measured. This process was repeated, and the injection pressure was increased by 0.5 or 1 MPa increments until more than 80% of the  $K_S$  was lost. The residual pressure inside the chamber was maintained to ensure that no refilling could occur during the measurements. We fitted a vulnerability curve by following the equation below (Pammenter & Vander Willigen 1998):

$$PLC = \frac{100}{1 + \exp(a(P - b))} \quad (1)$$

where  $PLC$  is the percentage loss of hydraulic conductivity,  $P$  is the applied pressure,  $b$  is the pressure causing 50% loss of hydraulic conductivity ( $-\psi_{50}$ ).

Leaf water potential at predawn ( $\psi_{pd}$ ) and midday ( $\psi_{md}$ ) of all the studied species was measured in the field using a pressure chamber (PMS) in the middle of the dry season. For each species, fully expanded mature leaves from three to five trees were collected, and  $\psi_{pd}$  measurements were proceeded at 6 : 00 am and completed before sunrise. For midday leaf

water potential, leaves exposed to direct solar radiation were collected, and  $\psi_{md}$  measurements were carried out between 12 : 30 and 14 : 00 pm. Stem hydraulic safety margin (SM) is defined as the difference between minimum stem water potential and the point which xylem tension inducing 50% loss of hydraulic conductivity ( $\psi_{md} - \psi_{50}$ ). SM indicates the degree of conservatism in a plant's hydraulic strategy, such that plants with narrow SM may face large potential risk of hydraulic failure (Choat *et al.* 2012).

Leaf turgor loss point ( $\psi_{tlp}$ ) is a key trait in assessing drought tolerance among species and biomes (Bartlett *et al.* 2012). Plants with high (less negative)  $\psi_{tlp}$  tend to close stomata early to avoid an excessive loss of cell water at low soil water availability (Brodrribb & Holbrook 2003).  $\psi_{tlp}$  was derived from the leaf pressure–volume relationships. Leaf-bearing branches from three to five individuals of each species were harvested and transferred to the laboratory where the basal ends of the branches were immersed in distilled water and re-cut. The branch samples were rehydrated until the leaf water potential was greater than  $-0.05$  MPa. Leaves were first weighed to obtain the initial fresh mass and then immediately placed in a pressure chamber to determine the initial water potential. Leaf mass and water potential were measured periodically during slow desiccation in the laboratory. Finally, leaves were oven-dried for 48 h at 70 °C to obtain their dry mass. Leaf water potential at turgor loss point ( $\psi_{tlp}$ ) was determined with a pressure–volume relationship analysis program developed by Schulte & Hinckley (1985).

### Statistical analysis

To test whether species abundance (measured as total basal area;  $\text{m}^2 \text{ha}^{-1}$ ) dynamics can be predicted by individual functional traits, we conducted a two-step statistical analysis. Firstly, we examined the response of species-specific total basal area to year using simple linear regressions. The coefficient of regression slope is referred to as 'abundance-year slope', and the variation of the regression coefficients as 'CV'. Steep abundance-year slopes indicate strong temporal trends of species abundance dynamics and CVs reflect the confidence boundaries of the relationships. Significant positive regression slopes indicated that species abundances increased ( $P < 0.05$ ). By contrast, significant negative regression slopes implied that species decreased in abundance ( $P < 0.05$ ), whereas non-significant regression slopes denoted that species underwent minimal change ( $P \geq 0.05$ ). Before data analysis, all data were standardised such that species differing in abundance could be compared (Lasky *et al.* 2015):

$$z_i = \frac{x_i - \bar{x}}{\sigma_x} \quad (2)$$

where  $z_i$  is the standardised data,  $x_i$  is the abundance of a given species in year  $i$ ,  $\bar{x}$  is the mean value of the species abundance of the eight community surveys, and  $\sigma_x$  represents the standard deviation of the species abundance.

Secondly, we tested whether the species-specific responses could be predicted by plant functional traits. We performed weighted least-squares regressions with species-specific abundance-year slope as the response variable and trait values

(averaged from multiple samples) of individual species as predictor. The weights of the response and predictor variables for individual pairs were the inverse of the CVs of the abundance-year slopes, allowing species with more significant abundance–year relationships to have larger weights in the analysis (Soudzilovskaia *et al.* 2013). Additionally, we examined whether individual trait values differed among species groups that had different qualitative trends, that is, increase, decrease or non-significant change over time using one-way analysis of variance (ANOVA).

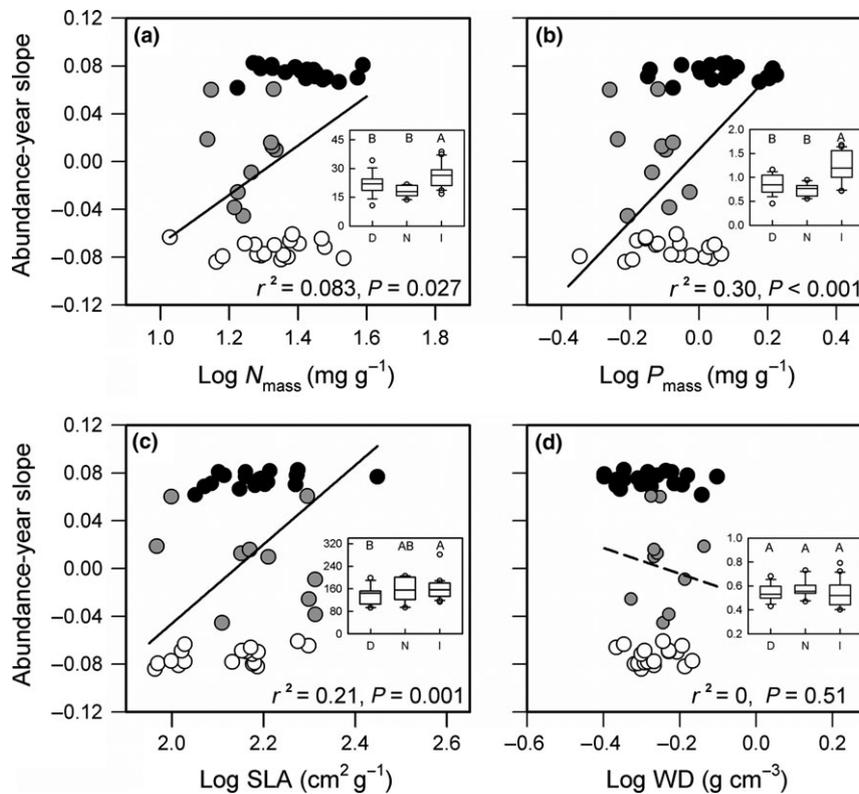
To better meet the assumptions of normality and homogeneous variances, both abundance and trait values were transformed by base 10 logarithm. To examine multivariate associations among the traits, we used principal component analysis (PCA). The relationships between species loadings on the first two PCA axes and abundance-year slopes of individual species were then analysed with weighted least-squares regressions. Mean factor loading values of the three species groups showed different trends in abundance (increase, decrease or non-significant change) on the first two axes were also tested by one-way ANOVA, to examine whether the three species groups differed significantly along the PCA axes. All data used in the analyses are provided as Supporting Information in Appendix S1. All the analyses were conducted in R 3.20 (R Foundation for Statistical Computing).

## RESULTS

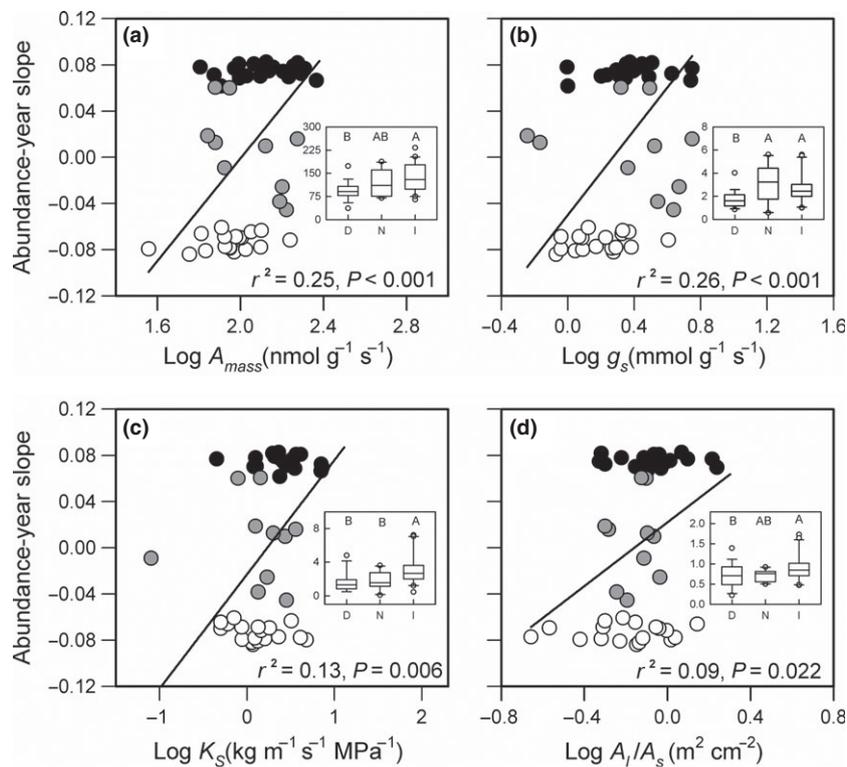
Among the 48 tree species investigated in this study, 18 species showed significant decreases in their abundance, 10 species had no significant change, and the abundance of 20 species increased significantly during the course of the present study (Appendix S1). We found that  $N_{mass}$ ,  $P_{mass}$  and SLA were positively correlated with the abundance-year slopes, and species that exhibited increases in abundance had significantly higher values (on average) of  $N_{mass}$ ,  $P_{mass}$ , and SLA than species that showed decreases in abundance (Fig. 1a–c), whereas non-significant correlations were observed between WD and the changes in species abundance over time (Fig. 1d).

For photosynthesis traits, the relationships between abundance-year slopes and  $A_{mass}$  and  $g_s$  were positively correlated, and species that increased in abundance on average had significantly higher  $A_{mass}$  and  $g_s$  than species that decreased in abundance (Fig. 2a, b). Similar patterns were found for hydraulic traits, where  $K_S$  and  $A_i/A_s$  were positively correlated with the abundance-year slopes, and species that increased in abundance on average had significantly higher  $K_S$  and  $A_i/A_s$  than species that decreased in abundance (Fig. 2c, d).

With respect to drought tolerance traits, the abundance-year slopes were negatively correlated with  $\psi_{t1p}$  and  $\psi_{pd}$ , and species showed increases in abundance had significantly higher



**Figure 1** The relationships between functional traits and abundance-year slopes of individual species: (a) Leaf nitrogen concentration ( $N_{mass}$ ), (b) leaf phosphorus concentration ( $P_{mass}$ ), (c) specific leaf area (SLA), and (d) sapwood density (WD). White, grey, and black circles indicate species decrease, non-significant change, and increase in abundance, respectively. A dashed line denotes a non-significant relationship between trait and abundance-year slopes. Insets: differences in functional trait values among species groups with different trends in abundance. Species groups are: D, species decreased significantly in abundance ( $n = 18$  species); N, species had no significant change in abundance ( $n = 10$  species); I, species increased significantly in abundance ( $n = 20$  species). Boxplots represent median (line), 25–75 quartiles (boxes), 5th and 95th percentile values (error bars) and extreme values (circles), respectively. Different letters above column indicate a significant difference ( $P < 0.05$ ).



**Figure 2** The relationships between functional traits and abundance-year slopes of individual species: (a) maximum CO<sub>2</sub> assimilation rate per unit mass ( $A_{mass}$ ), (b) stomatal conductance per unit mass ( $g_s$ ), (c) sapwood-specific hydraulic conductivity ( $K_S$ ), and (d) leaf area/sapwood area ratio ( $A_l/A_s$ ). Insets: differences in functional trait values among species groups with different trends in abundance. Figure explanations are provided in Fig. 1.

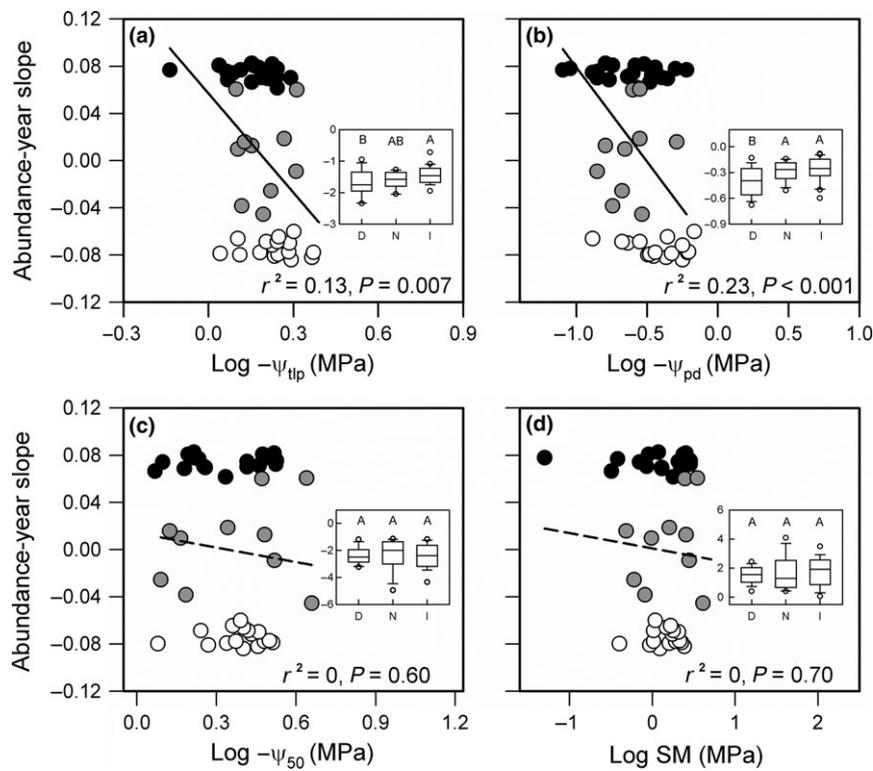
(less negative)  $\psi_{tlp}$  and  $\psi_{pd}$  than species displayed decreases in abundance (Fig. 3a, b). However, the abundance-year slopes were not significantly correlated with  $\psi_{50}$  and SM, and there were no differences in  $\psi_{50}$  and SM among species groups (Fig. 3c, d).

In order to analyse multivariate strategies of species, we conducted a principal component analysis (PCA) on 12 functional traits across the 48 species (Table S1). The first two principal components captured 44.1% of the variance, with 30.1% in the first axis (Fig. 4a). PCA axis 1 showed strong positive loadings for leaf nutrient concentrations ( $N_{mass}$  and  $P_{mass}$ ), photosynthetic-related traits ( $A_{mass}$  and  $g_s$ ) and stem hydraulic conductivity ( $K_S$ ), while WD and  $\psi_{tlp}$  were loaded at the negative end. The second axis explained 14.0% of the variation, and was primarily structured by  $\psi_{50}$ , SM and  $\psi_{pd}$  (Fig. 4b). We found that species loadings on the first two axes were significantly correlated with the abundance-year slopes, and that species groups with contrasting trends in abundance (decrease or increase) were well separated along the first two axes (Fig. 4c, d), indicating that the divergence of multiple functional traits loaded on the first two axes was closely associated with distinct trends in species abundance over time.

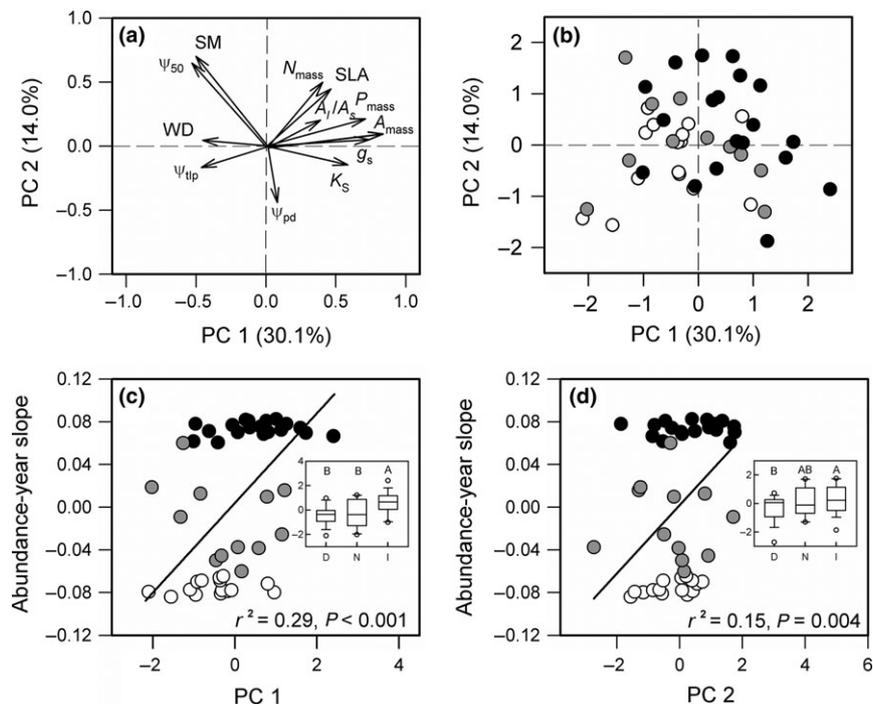
## DISCUSSION

Drought resulting from decreasing rainfall or increasing temperature (or both) may alter forest composition (Carnicer *et al.* 2011; Fauset *et al.* 2012). At our study site, although annual precipitation had not changed significantly during the

course of our study, the annual number of rain-free days had significantly increased, coupled with warming that increases evapotranspiration, resulting in significant decreases in soil moisture, particularly during the dry season (Fig. S1). We therefore expected that the climate change-induced soil drying combined with higher vapour pressure deficit (VPD) might impose a strong influence on the compositional shifts in this subtropical forest (Zhou *et al.* 2013). In the present study, we found that suites of functional traits displayed a tight association with the observed species temporal trends in abundance. We showed that species with high hydraulic conductivity (high  $K_S$  and  $A_l/A_s$ ) and carbon fixation rates (high  $A_{mass}$  and  $g_s$ ), low resource input into construction (high SLA) and a luxury nutrient use strategy (high  $N_{mass}$  and  $P_{mass}$ ) increased their abundance, whereas species with the opposite trait patterns decreased in abundance. For example, compared with species that had decreased in abundance, species with increasing abundances had on average 93% higher hydraulic conductivity, 46% higher photosynthesis rate, 44% higher leaf phosphorous concentration, 20% higher leaf nitrogen concentration and 18% higher specific leaf area (Table S2). Our results indicate that species with life histories for rapid growth (high  $N_{mass}$ ,  $P_{mass}$ , SLA,  $A_{mass}$ ,  $g_s$ ,  $K_S$ , and  $A_l/A_s$ ) increased their abundance over time. This directional change in species abundance is likely attributed to a combination of drier soil and higher VPD during the course of our study in this subtropical forest. Because under circumstances where water availability became critical in these habitats, traits associated with fast growth can confer a demographic advantage



**Figure 3** The relationships between functional traits and abundance-year slopes of individual species: (a) turgor loss point ( $\psi_{tlp}$ ), (b) predawn leaf water potential ( $\psi_{pd}$ ), (c) xylem tension at 50% loss of hydraulic conductivity ( $\psi_{50}$ ), and (d) hydraulic safety margin (SM). Insets: differences in functional trait values among species groups with different trends in abundance. Figure explanations are provided in Fig. 1.



**Figure 4** A principal component analysis on 12 functional traits of the 48 study species. (a) Loading plots for the first two axes; (b) species loadings on the first and second axes; (c-d) relationships between species loadings on the first two axes and abundance-year slopes of individual species. Insets: differences in functional traits among species groups with different trends in abundance. Figure explanations are provided in Fig. 1.  $N_{mass}$ , leaf nitrogen concentration;  $P_{mass}$ , leaf phosphorus concentration; WD, sapwood density; SLA, specific leaf area;  $A_{mass}$ , maximum  $CO_2$  assimilation rate per unit mass;  $g_s$ , stomatal conductance per unit mass;  $K_s$ , sapwood-specific hydraulic conductivity;  $A_l/A_s$ , leaf area/sapwood area;  $\psi_{tlp}$ , turgor loss point;  $\psi_{50}$ , xylem tension at 50% loss of hydraulic conductivity;  $\psi_{pd}$ , predawn leaf water potential; SM, stem hydraulic safety margin.

and allow for increased abundances, which are consistent with findings in a number of previous studies (Wright *et al.* 2004b; DeWalt *et al.* 2010; Enquist & Enquist 2011; Schnitzer & Bongers 2011; van der Sande *et al.* 2013).

As soil became drier and VPD increased, one would expect that species with more drought tolerance traits could increase in abundance over time. Indeed, we found species that increased in abundance had significantly less negative  $\psi_{\text{tlp}}$  than species that decreased in abundance. Species with less negative  $\psi_{\text{tlp}}$  tended to close stomata earlier than species with more negative  $\psi_{\text{tlp}}$  to prevent the risk of water loss and cavitation with decreasing water potential, thus making hydraulic failure less likely (Brodribb & Holbrook 2003; McDowell *et al.* 2011; Bartlett *et al.* 2012). Stomatal closure in species with less negative  $\psi_{\text{tlp}}$  may diminish their carbon assimilation (McDowell *et al.* 2008), but high  $K_S$  and  $A_{\text{mass}}$  of these species may allow species to conduct more photosynthesis in a shorter period of time during the dry season (Chen *et al.* 2015). Furthermore, we found species that increased in abundance had significant higher (less negative)  $\psi_{\text{pd}}$  than species that decreased in abundance during the dry season. The less negative values of  $\psi_{\text{pd}}$  indicate species maintained relatively better internal water status (Bucci *et al.* 2009), which would give them a competitive advantage (e.g. the maintaining of high photosynthesis rates) during the dry season and allow species to increase in abundance over time (Schnitzer 2005). In addition, we showed in an earlier study that this forest community is undergoing a transition with decreasing canopy individuals with large DBH and height (Zhou *et al.* 2013), which might be due to larger individuals that are more sensitive to drought stress than smaller individuals (Condit *et al.* 2004; Nepstad *et al.* 2007). As a result, more abundant sunlight can penetrate the canopy such that light availability to plants increase, and water deficit stress could be exacerbated due to increased evaporation associated with increased light availability. Under these conditions, species with both fast-growing (high  $A_{\text{mass}}$  and  $K_S$ ) and drought-tolerant traits (less negative  $\psi_{\text{tlp}}$  and  $\psi_{\text{pd}}$ ) are more likely to be the beneficiaries, as found in the present study.

We found no difference in xylem resistance to embolism ( $\psi_{50}$ ) among species with different trends in abundance. Species with more embolism-resistant xylem are presumably more successful at avoiding hydraulic failure (Meinzer *et al.* 2009). In the present study, however,  $\psi_{\text{pd}}$  of the 48 species in the mid-dry season (when drought in this subtropical forest was at its peak) was rather high ( $\sim -0.31$  MPa on average and the extreme value  $-0.68$  MPa; Appendix S1), indicating that the potential risk of hydraulic failure caused by climatic change-induced drought stress was low. Additionally, the majority of our study species operated over a relatively wide hydraulic safety margin ( $> 1.0$  MPa; Appendix S1), which might have made them less susceptible to decreasing soil moisture than species occurred in drought-prone habitats observed elsewhere (Choat *et al.* 2012). Thus, the lack of a significant correlation between  $\psi_{50}$  and species abundance dynamics might be due to the extensive capacity of trees to regulate plant water potential leading to a wide margin of safety against hydraulic failure in our forest.

Overall, our observed patterns between species abundance changes and functional trait variations under a drought-prone

environment, possibly due to warming and/or altered rainfall, tell a consistent story of community dynamics, which is dominated by increases in the abundance of species with life histories that are selected for more rapid resource capture (fast-growing) and more robust drought tolerance. We acknowledge some uncertainties and limitations in our data. Firstly, our forest, like all terrestrial ecosystems elsewhere, has also experienced rising atmospheric  $\text{CO}_2$  concentration and increased nitrogen deposition that might allow for fast-growing species with rapid resource acquisition strategies to increase in abundance over time, but contributions of these potential drivers to the temporal changes in species abundance could not be distinguished with our current data set. Secondly, successional recovery from past disturbance events can also be the causes underlying the directional changes in species abundance (Feeley *et al.* 2011), although our forest is more than 400 years old and had not experienced any noticeable disturbance during the course of our study, non-stand replacing disturbances could occur between the establishment of the forest and the time of plot establishment in 1978. While potential disturbance legacy remains to be examined, their impacts on this subtropical forest are likely minimal after more than several decades. Thirdly, we measured functional traits on three to five individuals with DBH comparable to the mean DBH value of a given species, which would potentially lead to bias in trait value collections, because trees at different canopy positions with different DBH size may respond differently to global change (da Costa *et al.* 2010; Phillips *et al.* 2010). Lastly, large trees were established well before our observation began in 1978, thus their dynamics (mortality) could be chiefly regulated by endogenous processes such as longevity. Hence, the relatively short time scales of the present study compared with long-term forest dynamics might limit the accuracy in forecasting global change impacts on tree species turnover. Yet, to our knowledge, our results provide a plausible functional basis for the observed temporal change in species abundance, demonstrating that functional traits are a good predictor of global change impact on tree species dynamics in this subtropical forest.

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## AUTHORSHIP

R.L. and Q.Y. designed research; R.L., S.Z., D.Z., and Q.Z. performed research; R.L., S.Z., R.J., G.Z., H.Y.H.C., and Q.Y. analysed data; R.L., S.Z., R.J., H.Y.H.C., and Q.Y. wrote the paper.

## REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M. *et al.* (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.*, 259, 660–684.
- Barber, V.A., Juday, G.P. & Finney, B.P. (2000). Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, 405, 668–673.
- Bartlett, M.K., Scoffoni, C. & Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol. Lett.*, 15, 393–405.
- Brienen, R.J., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J. *et al.* (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519, 344–348.
- Brodribb, T.J. & Holbrook, N.M. (2003). Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiol.*, 132, 2166–2173.
- Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C. & Arce, M.E. (2009). Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia*, 160, 631–641.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G. & Penuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl Acad. Sci. USA*, 108, 1474–1478.
- Chen, Y.J., Cao, K.F., Schnitzer, S.A., Fan, Z.X., Zhang, J.L. & Bongers, F. (2015). Water-use advantage for lianas over trees in tropical seasonal forests. *New Phytol.*, 205, 128–136.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R. *et al.* (2012). Global convergence in the vulnerability of forests to drought. *Nature*, 491, 752–755.
- Cochard, H., Cruziat, P. & Tyree, M.T. (1992). Use of positive pressures to establish vulnerability curves - further support for the air-seeding hypothesis and implications for pressure-volume analysis. *Plant Physiol.*, 100, 205–209.
- Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G. *et al.* (2004). Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J. Trop. Ecol.*, 20, 51–72.
- da Costa, A.C., Galbraith, D., Almeida, S., Portela, B.T., da Costa, M., Silva Junior, Jde A. *et al.* (2010). Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytol.*, 187, 579–591.
- DeWalt, S.J., Schnitzer, S.A., Chave, J., Bongers, F., Burnham, R.J., Cai, Z.Q. *et al.* (2010). Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, 42, 309–317.
- Enquist, B.J. & Enquist, C.A.F. (2011). Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. *Glob. Chang. Biol.*, 17, 1408–1424.
- Fauset, S., Baker, T.R., Lewis, S.L., Feldpausch, T.R., Affum-Baffoe, K., Foli, E.G. *et al.* (2012). Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecol. Lett.*, 15, 1120–1129.
- Feeley, K.J., Davies, S.J., Perez, R., Hubbell, S.P. & Foster, R.B. (2011). Directional changes in the species composition of a tropical forest. *Ecology*, 92, 871–882.
- Lasky, J.R., Bachelot, B., Muscarella, R., Schwartz, N.B., Forero-Montaña, J., Nytech, C.J. *et al.* (2015). Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology*, 96, 2157–2169.
- Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S. *et al.* (2004). Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 359, 421–436.
- Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A. & Laurance, W.F. (2009). Changing ecology of tropical forests: evidence and drivers. *Annu. Rev. Ecol. Evol. Syst.*, 40, 529–549.
- Luo, Y. & Chen, H.Y.H. (2013). Observations from old forests underestimate climate change effects on tree mortality. *Nat. Commun.*, 4, 1655.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z. *et al.* (2009). Widespread increase of tree mortality rates in the western United States. *Science*, 323, 521–524.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T. *et al.* (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.*, 178, 719–739.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F. & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.*, 26, 523–532.
- Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A. & Woodruff, D.R. (2009). Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Funct. Ecol.*, 23, 922–930.
- Mouillot, D., Graham, N.A., Villegier, S., Mason, N.W. & Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.*, 28, 167–177.
- Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J. *et al.* (2003). Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, 300, 1560–1563.
- Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P. & Cardinot, G. (2007). Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, 88, 2259–2269.
- Pammenter, N.W. & Vander Willigen, C. (1998). A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol.*, 18, 589–593.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37, 637–669.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F. *et al.* (2004). Pattern and process in Amazon tree turnover, 1976–2001. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 359, 381–407.
- Phillips, O.L., van der Heijden, G., Lewis, S.L., Lopez-Gonzalez, G., Aragao, L.E., Lloyd, J. *et al.* (2010). Drought-mortality relationships for tropical forests. *New Phytol.*, 187, 631–646.
- Poorter, L., McDonald, I., Alarcon, A., Fichtler, E., Licona, J.C., Pena-Claros, M. *et al.* (2010). The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol.*, 185, 481–492.
- Potvin, C. & Gotelli, N.J. (2008). Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecol. Lett.*, 11, 217–223.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997). From tropics to tundra: global convergence in plant functioning. *Proc. Natl Acad. Sci. USA*, 94, 13730–13734.
- van der Sande, M.T., Poorter, L., Schnitzer, S.A. & Markesteijn, L. (2013). Are lianas more drought-tolerant than trees? A test for the role of hydraulic architecture and other stem and leaf traits. *Oecologia*, 172, 961–972.
- Schnitzer, S.A. (2005). A mechanistic explanation for global patterns of liana abundance and distribution. *Am. Nat.*, 166, 262–276.
- Schnitzer, S.A. & Bongers, F. (2011). Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecol. Lett.*, 14, 397–406.

- Schulte, P.J. & Hinckley, T.M. (1985). A comparison of pressure-volume curve data-analysis techniques. *J. Exp. Bot.*, 36, 1590–1602.
- Shen, C., Liu, D., Peng, S., Sun, Y., Jiang, M., Yi, W. *et al.* (1999).  $^{14}\text{C}$  measurement of forest soils in Dinghushan Biosphere Reserve. *Chin. Sci. Bull.*, 44, 251–256.
- Soudzilovskaia, N.A., Elumeeva, T.G., Onipchenko, V.G., Shidakov, I.I., Salpagarova, F.S., Khubiev, A.B. *et al.* (2013). Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proc. Natl Acad. Sci. USA*, 110, 18180–18184.
- Sperry, J.S., Donnelly, J.R. & Tyree, M.T. (1988). A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ.*, 11, 35–40.
- Van Bodegom, P.M., Douma, J.C., Witte, J.P.M., Ordoñez, J.C., Bartholomeus, R.P. & Aerts, R. (2012). Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: exploring the merits of traits-based approaches. *Glob. Ecol. Biogeogr.*, 21, 625–636.
- Wang, B. & Ma, M. (1982). The successions of the forest community in Dinghushan. *Trop. Subtrop. For. Ecosyst. Res.*, 1, 142–156.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004a). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Wright, S.J., Calderón, O., Hernández, A. & Paton, S. (2004b). Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology*, 85, 484–489.
- Zhou, G., Wei, X., Wu, Y., Liu, S., Huang, Y., Yan, J. *et al.* (2011). Quantifying the hydrological responses to climate change in an intact forested small watershed in Southern China. *Glob. Chang. Biol.*, 17, 3736–3746.
- Zhou, G., Peng, C., Li, Y., Liu, S., Zhang, Q., Tang, X. *et al.* (2013). A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China. *Glob. Chang. Biol.*, 19, 1197–1210.
- Zhou, G., Houlton, B.Z., Wang, W., Huang, W., Xiao, Y., Zhang, Q. *et al.* (2014). Substantial reorganization of China's tropical and subtropical forests: based on the permanent plots. *Glob. Chang. Biol.*, 20, 240–250.
- Zhu, S., Song, J., Li, R. & Ye, Q. (2013). Plant hydraulics and photosynthesis of 34 woody species from different successional stages of subtropical forests. *Plant Cell Environ.*, 36, 879–891.

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