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Increasing active biomass carbon may lead to a breakdown of mature forest equilibrium

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The finding that mature forest ecosystems increase carbon in woody tissues and mineral soils indicates that the original equilibriums are being pushed to a higher state. The final driving forces will probably be increasing CO₂ and nitrogen deposition, global warming, and changes to precipitation patterns. However, which part of a mature forest bears the direct impacts of environmental changes and reactivates the balanced ecosystem processes remains unclear. Here, we investigated the living biomass of mature forests in the tropical and subtropical biomes in China and found that active organs and small individuals have accumulated carbon at a rate of 203 kg C ha⁻¹ yr⁻¹ in recent decades, whereas the woody tissues did not display carbon accumulation with statistical significance. Our findings indicate that the increased labile plant inputs may have shifted mature forests from their previous equilibrium and caused them to enter a new non-equilibrium state.

Mature forests are considered to be carbon-neutral as well as to be in balanced states for all other ecosystem processes¹, including the process that links living biomass to soil organic carbon. Previous studies have demonstrated that the carbon in the biomass of boreal, temperate, and tropical old-growth forests and the soil organic carbon in subtropical old-growth forests² have increased over recent decades^{3–6}. In these previous studies, the biomass carbon refers only to the “inactive carbon” that is stored in the woody tissues of large trees^{5–7}; it does not include the biomass carbon in active organs (leaves, roots) and small individuals (small arbor and shrub, or small diameter at breast height (DBH) trees) that can also be considered “active carbon”.

Differences in some ecosystem functions between active and inactive biomass carbon are apparent. Table 1 presents some characteristics of the two classifications that relate to this study.

Although active carbon does not appear to have a role in mitigating the rising atmospheric CO₂ due to its short residence time, it plays an irreplaceable role in ecosystem processes^{8–9} involving the formation of ecosystem net productivity (NEP)^{10–11}. Increased active carbon in a mature forest may imply a reactivation of the ecosystem functions that can drive the mature forest into a new equilibrium. Ignoring changes in the active carbon may lead to a failure to address a new phenomenon that was previously considered to not occur in mature forests. For instance, the mechanism of increasing biomass carbons in boreal, temperate, and tropical old-growth forests¹² and soil organic carbon in subtropical old-growth forests² could be hardly addressed. Until now, no attention has been paid to the roles that active biomass carbon might play in mature forest ecosystem processes, and no studies have investigated the directional changes of the biomass carbon in active organs and small individuals of mature forests.

Here, we searched for directional changes in living biomass in mature forests located in the biomes of China's tropical forests and subtropical evergreen broadleaved forests (TEBFs) (Fig. 1) that compose more than 26% of China's terrestrial land area¹³. The main aim of this study was to partition the biomass of mature forests into active and inactive biomass carbon pools and understand their respective change trends.

Results

Trends of active and inactive biomass carbon pools. As shown in Fig. 2, among the 20 permanent plots in China's tropical/subtropical biome, the total biomass of entire stands did not display a significant increase ($p=0.132$) from 1978 to 2012. In addition, the total biomass in branches and stems, arbor, and DBH classes III and IV did not display significant increases ($p>0.225$). However, marked changes in the standing biomasses were observed in the leaves, roots, shrubs, and small arbores and DBH classes I and II, in which the biomasses

**Table 1 | Classifications and descriptions for active biomass carbon and inactive biomass carbon**

Carbon pools	Classification	Response time to environmental changes	Carbon residence time	Dominant substrate quality
Active carbon	leaves and roots; small arbores and shrubs; small-DBH individuals	Months to a few years	<10 years	carbohydrates, lipids and others with high nitrogen content
Inactive carbon	stems and branches; arbores; large-DBH individuals	>10 years	10 to hundreds of years	lignin, cellulose, and others with low nitrogen content

have all increased significantly ($p < 0.017$) for more than three decades. Therefore, this group displayed a trend similar to that of the entire stand but with statistical significance. This difference may be due to the fact that the biomasses in the leaves, roots, shrubs, and small arbor and DBH classes I and II amount to a small proportion of the entire stands. In the 20 permanent plots of mature forests, the average percentages of biomass in the leaves and roots, shrubs and small arbores and DBH classes I and II were only 20.6%, 7.2%, and 5.9%, respectively. Therefore, even a significant change in the biomasses of these components would not affect the statistical significance of the overall trends in the entire stand.

By partitioning the biomass into different organs for shrub, small arbor, and arbor (Fig. 3), we found that the biomasses in the stems, branches, leaves, and roots of arbor remained unchanged but the biomasses in all of the organs of both the shrubs and small arbores increased significantly. This result confirmed the finding¹⁴ that China's TEBF biomes are transitioning from cohorts of fewer and larger individuals to cohorts of a greater number of smaller individuals. The ecosystem may gradually be entering a lower non-equilibrium state because the shrub and small arbor groups would store less carbon than the arbor group.

Quantity of sequestered biomass carbon in active organs and small individuals. Table 2 illustrates that yearly biomass increments in leaves and roots were 92 and 295 kg ha⁻¹ yr⁻¹, respectively; those in shrubs and small arbores were 26 and 394 kg ha⁻¹ yr⁻¹, respectively, and those in DBH classes I and II were 139 and 273 kg ha⁻¹ yr⁻¹, respectively. In total, yearly biomass increments in organs, functional groups, and DBH classes were 387, 420, and 412 kg ha⁻¹ yr⁻¹, respectively, averaging 406 kg ha⁻¹ yr⁻¹ in dry matter.

If we assume that the carbon content is 50%, the yearly increase in active carbon in the mature forests of China's TEBF biomes was 203 kg C ha⁻¹ yr⁻¹ over more than three decades, which yields a

yearly sequestered carbon amount of 0.012 Pg C yr⁻¹ for the 5935.66 × 10⁴ ha¹⁵ of natural forest in China's tropical and subtropical regions. This value is equivalent to the estimation of all of China's natural forests by Fang *et al.*⁷ during the same period. The value was estimated in accordance with the long-term observations in mature forests and should be considerably smaller than the amount of carbon that can be sequestered by the natural forests of the area because most of the natural forests have not reached the ages of mature forests and are still in prior stages of development.

Discussion

Directional changes in biomass, composition and structure of China's TEBF biomes. We have previously found that China's TEBF biomes are transitioning from cohorts of fewer, larger individuals to ones with a higher number of smaller individuals^{14,16–17}. This trend was characterized by an increased number of individuals and species for the shrub and small arbor groups and a decreased number of individuals and species for the arbor group^{14,17}. In these studies, we elaborated the connections of the trends in structure and composition with global changes (global warming and precipitation pattern changes) and their consequent climate and soil drying.

In the present study, we further demonstrate that the reorganization in structure and composition has led the biomass carbon in leaves, roots, and small individuals (shrubs and small arbores, DBH classes I and II) to a directional change. We did not find that the biomass carbon in the entire stands as well as in branches, stems, and large individuals (inactive carbon) increase significantly. However, the biomass carbon in leaves, roots, and small individuals (shrubs and small arbores, DBH classes I and II) (active carbon) have been accumulating rapidly over the past three decades. The results from some other studies can be taken as evidences of our finding. Piao *et al.*¹⁸ reported an increasing Normalized Difference Vegetation Index (NDVI) in the distribution area of China's TEBF biomes over the past decade. FACE experiments reported that litterfall

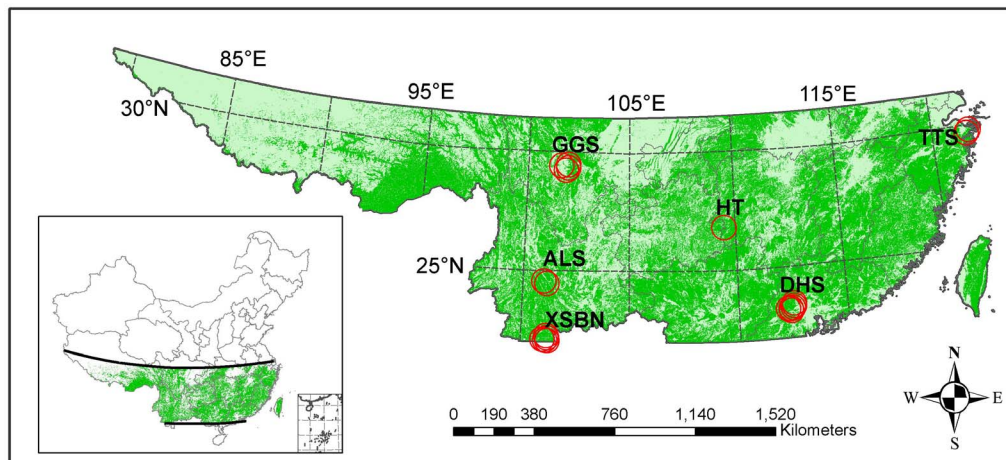


Figure 1 | Spatial distribution of the six field stations and the 20 permanently protected plots of mature forest across China's TEBF biome, generated using ArcGIS. The six field stations are TTS-Tiantongshan, DHS-Dinghushan, HT-Huitong, GGS-Gonggashan, XSN-Xishuangbanna, and ALS-Ailaoshan.

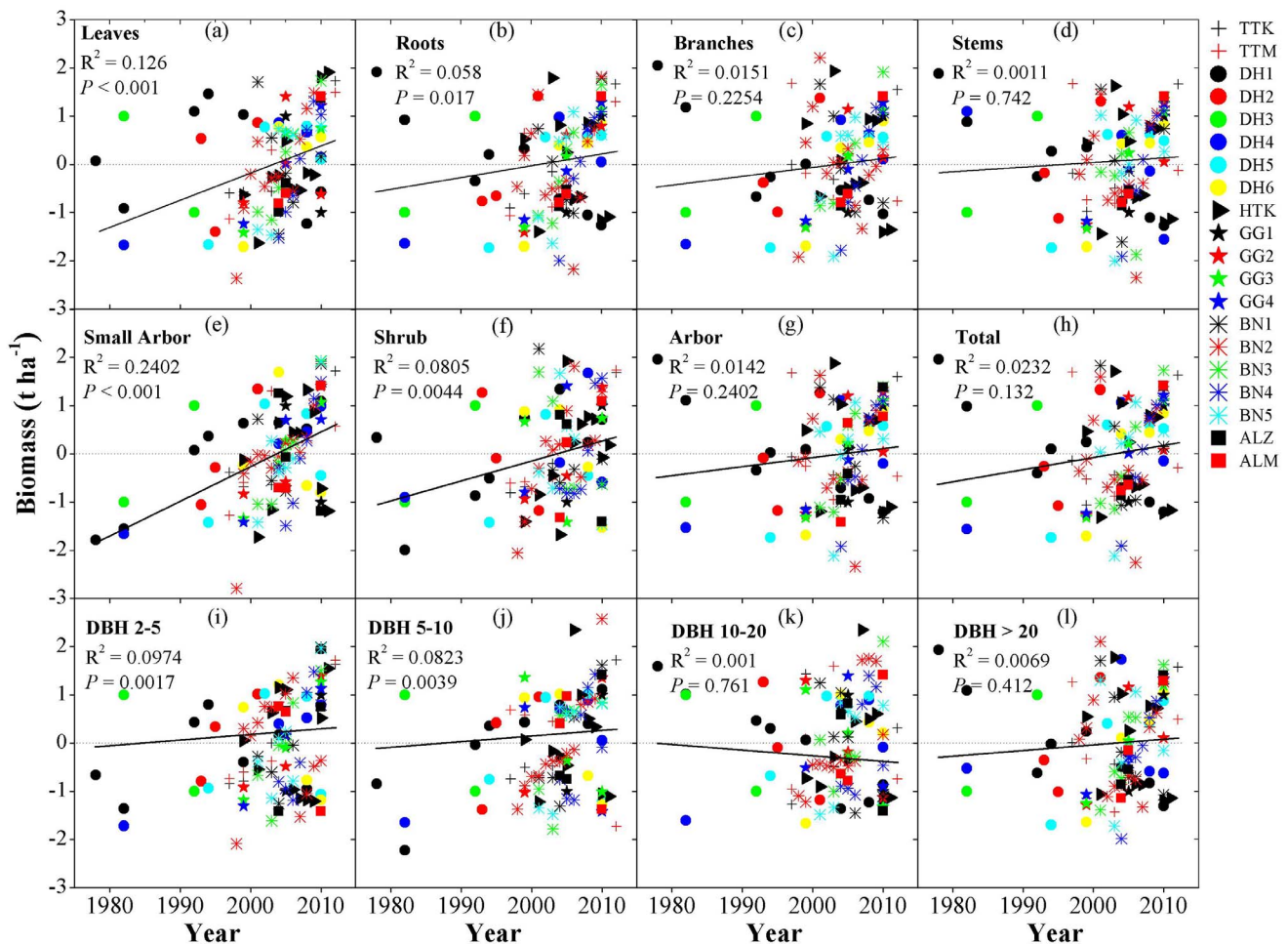


Figure 2 | Compound temporal trends in the biomass of the 20 permanently protected plots from 1978 to 2012. The top row (panel (a)–(d)) is classified according to organs; the middle row (panel (e)–(h)) is classified according to functional groups; the bottom row (panel (i)–(l)) is classified according to DBH classes. For comparison, all original data ($n=99$ in 20 plots) were standardised to the presented data with the averages and standard deviations in each plot being zero and one, respectively.

increased with elevated atmospheric CO_2 concentrations^{19–23} and predicted that changes in rainfall distribution patterns²⁴ and temperature²⁵ would also affect litterfall by altering leafing phenology²⁶. The results imply that active biomass carbon was increased both in natural conditions and in FACE experiments.

Connections between active and inactive biomass carbon pools.

Theoretically, the active biomass carbon pool plays the role of a transitional pool of photosynthesis products, which initiate all ecosystem processes. Partitioning the biomass carbon of a forest into two pools is important for addressing the mechanisms of non-equilibrium phenomena that are occurring in mature forests. Active biomass carbon is the outset of all biomass accumulation processes required to strengthen the connections between the changing environments and inactive carbon. The observed increase of inactive biomass carbon pools in intact African tropical forests is considered to be accompanied by a significant increase in the active biomass carbon pool⁶. In the present study, the biomasses in leaves and roots of both shrub and small arbor displayed significant increases, resulting in consistently significant increases in stems, branches and the entire functional groups of both shrub and small arbor. Correspondingly, for functional group of arbor, the biomasses in all organs and entire functional group did not display significant increases (Fig. 3). The results show that a positive relation between active and inactive biomass carbon pools in each functional group does exist. We suppose one of the reasons why the increased active

biomass carbon pool (leaves, roots, or small individuals) in mature forests of China's TEBF biomes did not result in a significant increase in the inactive biomass carbon pool of the entire stands is because its biomass amounts to a small part. However, more studies on the nexuses between the two pools would be necessary in the future.

Demands for the nexuses between active biomass carbon and soil organic carbon.

Soil organic carbon comes mainly from active biomass carbon. For aboveground and belowground processes, most of the active organs and small individuals complete their physiological functions in a few years, fall into the soil as fine litter, and activate complex belowground processes²⁷. In addition, after tens and hundreds of years, a small part of the inactive carbon may be artificially removed from the forest and thus lose its ecosystem functions; the remaining part of the inactive carbon will fall into the soil as coarse litter²⁸. Fine litter may play a more important role in activating ecosystem processes than coarse litter. Studies have shown that litter with different sizes and organs decay at different rates^{29–31} and in turn influence the fraction of biomass carbon that move into the mineral soils³². Compared to coarse litter from stems and branches, fine litter that originates from leaves and roots would enhance the fractions of biomass carbon moving into mineral soils due to their higher nitrogen content and lower lignin content^{28–35}. However, the effects of fresh carbon input to soil on soil carbon content has been highly controversial since 1926^{36–37}. Many studies have demonstrated a negative relationship between carbon input and

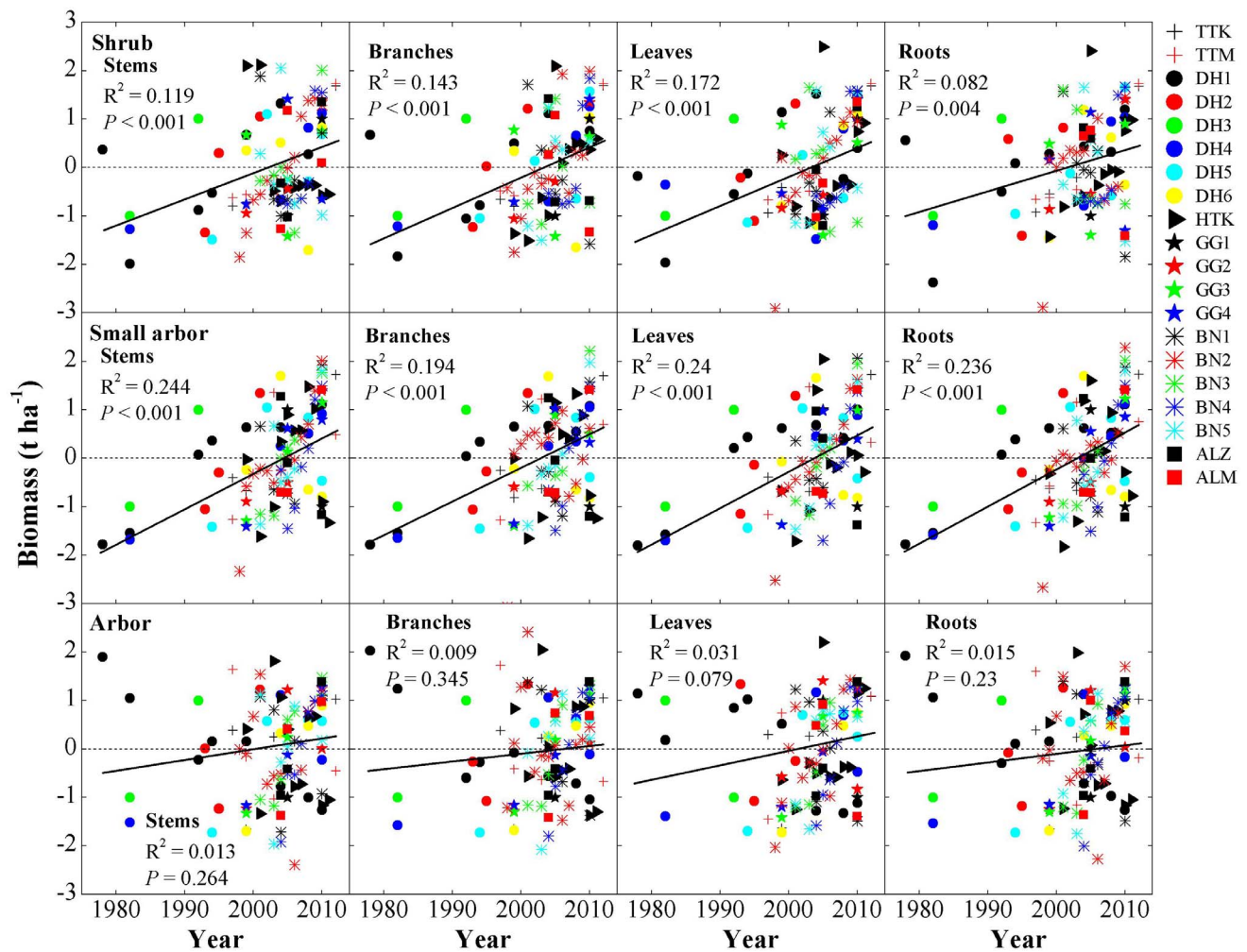


Figure 3 | Compound temporal trends of the biomass of various organs for each functional group from 1978 to 2012. For comparison, all original data ($n=99$ in 20 plots) were standardised to the presented data with the averages and standard deviations in each plot being zero and one, respectively.

soil carbon conservation^{26,37–39}, which contradicts the traditional concepts^{10–11}. Other studies still suggest the traditional conclusions³⁵, depending on the vegetation types and environmental factors in wet tropical forests^{40–42}. Notably, Cotrufo *et al.*³⁵ confirmed a nexus between labile plant inputs and stable soil organic matter. Several observed increases in soil organic carbon in China's TEBF biomes have also been confirmed to be closely related to active carbon pools^{2,32,43}. These studies have identified an urgent need to identify the states of active carbon pools in mature forests under changing environments to address the reactivation of belowground processes.

In the present study, we partitioned forest biomass carbon into active carbon and inactive carbon and found that the mature forests in China's TEBF biomes sequestered carbon in active carbon pools instead of inactive carbon pools. Our finding provides direct evidence that mature forests have been shifted from their previous equilibrium by more labile plant inputs and have entered a new non-equilibrium state. These findings highlight the need to partition forest biomass carbon into the active and inactive pools as well as the need for additional studies on the nexus between the two pools and soil organic carbon.

Table 2 | Linear mixed modelling equations of living biomass compounded from the 20 plots of mature forest

Category	Subdivision	Equations	P	Slope_std	Intercept_std
Organs	leaves	$y = 92.42x - 178,781$	<0.001	22.48	45,044
	roots	$y = 295.25x - 538,294$	0.024	128.13	256,694
	branches	$y = 223.67x - 382,211$	0.285	207.91	416,547
	stems	$y = 470.18x - 777,493$	0.215	376.57	754,441
Functional group	shrub	$y = 25.57x - 48,100$	0.01	24.46	48,999
	small arbor	$y = 393.97x - 771,463$	<0.001	93.33	187,025
	arbor	$y = 0.0020x + 268,870$	0.265	~	29,800
	Total	$y = 0.0026x + 289,540$	0.142	~	28,986
DBH	$2 \leq \text{DBH} \leq 5$ cm	$y = 139.28x - 136,624$	0.001	19.48	39,015
	$5 < \text{DBH} \leq 10$ cm	$y = 273.53x - 306,595$	0.004	52.99	106,195
	$10 < \text{DBH} \leq 20$ cm	$y = -0.705x + 37,379$	0.997	170.23	341,038
	$\text{DBH} > 20$ cm	$y = 0.0018x + 235,100$	0.463	~	33,215



Methods

Site description. The biomes of China's tropical forests and evergreen broadleaved forests (TEBFs) are distributed in the area from 21°N to 31°N in latitude and 101°E to 122°E in longitude. As the climax vegetation in this climate, TEBF dominates the direction in natural succession and recovery of all forests in the region¹³. At elevations higher than 2600 m, the original types of vegetation are *Abies fabri* (Mast) and mountain moss. Under the combined effects of the subtropical convergence and the uplift of the Himalayas, the monsoon climate prevails in this region, with a mean annual precipitation (MAP) of 1300–2000 mm, with nearly 80% falling in the wet season (April–September) and the other 20% falling in the dry season (October–March). The mean annual temperature (MAT) and relative humidity are 15.0–21.5°C and 78%, respectively. The environments in these plots differ significantly, as shown in Table S1.

The Chinese Academy of Sciences (CAS) and the Ministry of Science and Technology of P. R. China have arranged a series of field research stations across the region since the 1970s. Six of these field research stations (Tiantongshan TTS, Dinghushan DHS, Huitong HT, Gonggashan GGS, Xishuangbanna XSBN, and Ailaoshan ALS) have a total of 20 permanent monitoring plots (TTK, TTM, DH1, DH2, DH3, DH4, DH5, HTK, GG1, GG2, GG3, GG4, BN1, BN2, BN3, BN4, BN5, ALZ, and ALM) in the mature forests (Fig. 1, Table S1). When selecting permanent plots of matured forests, two procedures were involved to ascertain the plot's representativeness. First, the vegetation community structure and the composition of optional plots were studied to demonstrate that the forests were indeed mature. Second, various data were collected to demonstrate that the forest ecosystems had not been subject to artificial management and natural catastrophic events (e.g., landslides, typhoon, forest fires) for a sufficient period of time. Specifically, no trace of earlier management practices and no natural catastrophic events, including charcoal in the soils and tree stumps with fire scars or footprints of landslides and typhoons, could be observed. Moreover, soil profiles in the entire plot must be integrated and undisturbed. Regularly repeated censuses have been conducted since the establishment of each permanent plot using a unified methodology that was formulated by the Chinese Ecosystem Research Network.

Community surveys. All individuals with a diameter at breast height (DBH at 1.3 m above the ground) of at least 2 cm and a height of at least 1.5 m in the permanent sample plots were labelled in the first survey. Any newly recruited individuals who met these criteria were also labelled in the subsequent surveys. Each individual was assigned a unique number so that all individuals were accurately traced. During each survey, we identified the species of each labelled individual and measured the DBH and height.

Calculation of biomass. Forest biomasses were calculated using allometric equations that were established for each of the six stations. All of the allometric equations were subdivided into various organs (leaf, branch, stem, and root)^{44–49}.

Data standardisation. All of the calculated biomass data in each plot were standardised as follows:

$$x_{ij}' = \frac{x_{ij} - \bar{x}_i}{\delta_i} \quad (1)$$

where x_{ij}' is the standardised datum that correspond the original datum x_{ij} (dimensionless); i represents the 20 plots (i = TTK, TTM, DH1, DH2, DH3, DH4, DH5, DH6, HTK, GG1, GG2, GG3, GG4, BN1, BN2, BN3, BN4, BN5, ALZ, and ALM); j is the census year from 1978 to 2012; \bar{x}_i is the mean of the measurement values from 1978 to 2012 for plot i ; and δ_i is the standard deviation of the measurement values from 1978 to 2012 for plot i .

Data compiling. All species were classified into one of three functional groups (arbor, small arbor, and shrub) according to the “Flora of China” records⁵⁰, which was based on genetic characteristics of a given species. Hence, if a particular species belonged to shrub, small arbor, or arbor, for example, both its juvenile and mature individuals were given the same functional group classification. All individuals were also classified into one of four DBH classes (I: $2 \leq \text{DBH} \leq 5$ cm; II: $5 < \text{DBH} \leq 10$ cm; III: $10 < \text{DBH} \leq 20$ cm and IV: $\text{DBH} > 20$ cm). We analysed all of the data according to the three hierarchies: I organ or functional group or DBH class → II plot → III survey year. Data were standardised in each plot, and the standardised data across all plots were subsequently analysed for statistical trends.

Statistical analysis. A simple linear regression model was used to analyse statistical trends for the standardised biomass data of the 20 plots. A linear mixed-effects model (LMM) with random effects was applied to the original biomass data to obtain the yearly accumulated biomasses.

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Author contributions

Y.X. analysed the data and wrote the manuscript. G.Z. designed the study and proposed the scientific hypothesis. Q.Z. compiled the data. W.W. performed the correlation analysis and developed the figures. S.L. compiled the data for Dinghushan.

Additional information

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