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 processes, 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 forests have increased over recent decades. In these previous studies, the biomass carbon refers only to the “inactive carbon” that is stored in the woody tissues of large trees; 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 involving the formation of ecosystem net productivity (NEP). 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 forests and soil organic carbon in subtropical old-growth forests 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 area. 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 biomass were observed in the leaves, roots, shrubs, and small arbores and DBH classes I and II, in which the biomasses...
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 finding that China’s TEBF biomes are transitioning from cohorts of fewer, larger individuals to ones with a higher number of smaller individuals. 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. 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

**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 |

**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. 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. 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.

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increased with elevated atmospheric CO2 concentrations and predicted that changes in rainfall distribution patterns and temperature would also affect litterfall by altering leafing phenology. 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 nonequilibrium 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 pool. 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 processes. 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 litter. 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 and in turn influence the fraction of biomass carbon that move into the mineral soils. 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. However, the effects of fresh carbon input to soil on soil carbon content has been highly controversial since 1926. Many studies have demonstrated a negative relationship between carbon input and
soil carbon conservation\textsuperscript{26,37–39}, which contradicts the traditional concepts\textsuperscript{10–11}. Other studies still suggest the traditional conclusions\textsuperscript{35}, depending on the vegetation types and environmental factors in wet tropical forests\textsuperscript{40–42}. Notably, Cotrufo \textit{et al.}\textsuperscript{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\textsuperscript{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 sequestrated 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.

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.

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≤DBH≤5 cm        | \(y = 139.28x + 136,624\)                                               | 0.001       | 19.48     | 39,015        |
|                | 5<DBH≤10 cm       | \(y = 273.53x + 306,595\)                                               | 0.004       | 52.99     | 106,195       |
|                | 10<DBH≤20 cm      | \(y = -0.705x + 37,379\)                                                | 0.997       | 170.23    | 341,038       |
|                | DBH>20 cm         | \(y = 0.0018x + 235,100\)                                               | 0.463       | ~         | 33,215        |
4. Chave, J. Statistical analysis of biomass data. Nature 455, 213–215 (2008).

5. Lewis, S. L. et al. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006 (2009).

6. Fang, J. Y., Chen, A. P., Peng, C. H., Zhao, S. Q. & Qi, L. J. Changes in forest biomass carbon storage in China between 1949 and 1998. Science 292, 2320–2322 (2001).

7. Sayer, E. J., Tanner, E. V. J. & Chessman, A. W. Increased litterfall changes fine root distribution in a moist tropical forest. Plant Soil 281, 5–13 (2006).

8. Högborg, P. et al. High temporal resolution tracing of photosynthetic carbon from the tree canopy to forest soil microorganisms. New Phytol. 177, 220–228 (2008).

9. Karlen, D. L. & Cambardella, C. A. Conservation strategies for improving soil quality and organic matter storage. Structure and Organic Matter Storage in Agricultural Soils. Carter, R. & Stewart, B. A. (ed.), 395–420 (CRC Press, Boca Ratón, 1996).

10. Parton, W. J., Ojima, D. S. & Schimel, D. S. Models to evaluate soil organic matter storage and dynamics. Structure and Organic Matter Storage in Agricultural Soils. Carter, R. & Stewart, B. A. (ed.), 420–448 (CRC Press, Boca Ratón, 1996).

11. Muller-Landau, H. C. Sink in the African jungle. Nature 457, 969–970 (2009).

12. The editorial board of vegetation of China. Vegetation of China 1 (Science Press, Beijing, China, 1980).

13. Zhou, G. Y. et al. Substantial reorganization of China’s tropical and subtropical forests: based on the permanent plots. Glob. Change Biol. 20, 240–250 (2014).

14. The editorial board of Reports on China’s Forest Resources. Reports on China’s Forest Resources—The Seventh National Survey on Forest Resources. (State Forestry Administration, PR China, 2009).

15. Zhou, G. Y. et al. Quantifying the hydrological responses to climate change in an intact forested small watershed in Southern China. Glob. Change Biol. 17, 3736–3746 (2011).

16. Zhou, G. Y. et al. A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China. Glob. Change Biol. 19, 1197–1210 (2013).

17. Piao, S. L. et al. Interannual variations of monthly and seasonal normalized difference vegetation index (NDVI) in China from 1982 to 1999. J. Geophys. Res. 108 (2003).

18. DeLucia, E. H. et al. Net primary production of a forest ecosystem with experimental CO2 enrichment. Science 284, 1177–1179 (1999).

19. Allen, A. S. et al. Effects of free-air CO2 enrichment (FACE) on belowground processes in a Pinus taeda forest. Ecol. Appl. 10, 437–448 (2000).

20. Finzi, A. C., Allen, A. S., DeLucia, E. H., Ellsworth, D. S. & Schlesinger, W. H. Forest litter production, chemistry, and decomposition following two years of free-air CO2 enrichment. Ecology 82, 470–484 (2001).

21. Schlesinger, W. H. & Lichter, J. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO2. Nature 411, 466–469 (2001).

22. Zak, D. R., Holmes, W. E., Finzi, A. C., Norby, R. J. & Schlesinger, W. H. Soil nitrogen cycling under elevated CO2: a synthesis of forest FACE experiments. Ecol. Appl. 13, 1508–1514 (2003).

23. Zhang, X. et al. Detection of human influence on twentieth-century precipitation trends. Nature 448, 462–465 (2007).

24. Raich, J. W., Russell, A. E., Kitayama, K., Parton, W. J. & Vitousek, P. M. Temperature influences carbon accumulation in moist tropical forests. Ecology 87, 76–87 (2006).

25. Sayer, E. J., Powers, J. S. & Tanner, E. V. J. Increased litterfall in tropical forests boosts the transfer of soil CO2 to the atmosphere. PLoS One 2, e1299 (2007).

26. Zhou, G. Y. et al. Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. Plant Ecol. 188, 77–89 (2007).

27. Yang, F. F. et al. Dynamics of coarse woody debris and decomposition rates in an old-growth forest in lower tropical China. For. Ecol. Manage. 259, 1666–1672 (2010).

28. Zhang, D. Q., Hui, D. F., Luo, Y. Q. & Zhou, G. Y. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93 (2008).

29. Zhou, G. Y. et al. Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. Plant Soil 311, 61–72 (2008).

30. Makkonen, M. et al. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. Ecol. Lett. 15, 1033–1041 (2012).

31. Huang, Y. et al. Controls of litter quality on the carbon sink in soils through partitioning the products of decomposing litter in a forest succession series in South China. For. Ecol. Manage. 261, 1170–1177 (2011).

32. Bruckman, V. J., Yan, S., Hochbichler, E. & Glässl, G. Carbon pools and temporal dynamics along a rotation period in Quercus robur dominated high forest ecosystems with standards stands. For. Ecol. Manage. 262, 1853–1862 (2011).

33. Gul, S., Whalen, J. K., Ellis, B. E. & Mustafa, A. F. Influence of plant residue chemistry on soil CO2-C production: A study with Arabidopsis thaliana cell walls grown on KNA77, MTW-10 and CCR1. Pedobiologia 55, 349–356 (2012).

34. Cotrufo, M.F., Wallenstein, M.D., Root, C.M., Denef, K. & Paul, E. The Microbial Efficiency- Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Glob. Change Biol. 19, 988–995 (2013).
36. Löhnis, F. Nitrogen availability of green manures. Soil Sci. 22, 253–290 (1926).
37. Fontaine, S., Bardoux, G., Abbadie, L. & Mariotti, A. Carbon input to soil may decrease soil carbon content. Ecol. Lett. 7, 314–320 (2004).
38. Högberg, P. et al. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792 (2001).
39. Gill, R. A. et al. Nonlinear grassland responses to past and future atmospheric CO₂. Nature 417, 279–282 (2002).
40. Li, Y. Q., Xu, M., Sun, O. J. & Cui, W. C. Effects of root and litter exclusion on soil CO₂ efflux and microbial biomass in wet tropical forests. Soil Biol. Biochem. 36, 2111–2114 (2004).
41. Schaefer, D. A., Feng, W. T. & Zou, X. M. Plant carbon inputs and environmental factors strongly affect soil respiration in a subtropical forest of southwestern China. Soil Biol. Biochem. 41, 1000–1007 (2009).
42. Leff, J. W. et al. Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. Glob. Change Biol. 18, 2969–2979 (2012).
43. Tang, X. L. et al. Different patterns of ecosystem carbon accumulation between a young and an old-growth subtropical forest in Southern China. Plant Ecol. 212, 1385–1395 (2011).
44. Cheng, G. W. & Wang, G. X. Long-Term Data Sets of Monitoring and Researches on Chinese Ecosystems: Volume of Forest Ecosystem-Gonggashan Station, Sichuan province (1995–2006). (China Agriculture Press, Beijing, China, 2011).
45. Deng, X. B. & Tang, I. W. Long-Term Data Sets of Monitoring and Researches on Chinese Ecosystems: Volume of Forest Ecosystem-Xishuangbanna Station, Yunnan province (1998–2006). (China Agriculture Press, Beijing, China, 2011).
46. Wang, S. L. Long-Term Data Sets of Monitoring and Researches on Chinese Ecosystems: Volume of Forest Ecosystem-Huitong Station, Hunan province (1960–2006). (China Agriculture Press, Beijing, China, 2011).
47. Wang, X. H. Long-Term Data Sets of Monitoring and Researches on Chinese Ecosystems: Volume of Forest Ecosystem-Tiantongshan Station, Zhejiang province (1983–2009). (China Agriculture Press, Beijing, China, 2011).
48. Zhang, Q. M. Long-Term Data Sets of Monitoring and Researches on Chinese Ecosystems: Volume of Forest Ecosystem-Dinghushan Station, Guangdong province (1998–2008). (China Agriculture Press, Beijing, China, 2011).
49. Zhang, Y. P. & Liu, Y. H. Long-Term Data Sets of Monitoring and Researches on Chinese Ecosystems: Volume of Forest Ecosystem-Ailaoshan Station, Yunnan province (2003–2007). (China Agriculture Press, Beijing, China, 2011).
50. The editorial board of flora of China. Flora of China. (Science Press. Beijing, China, 2004).

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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.

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