

# Impact of Rising Temperatures on the Biomass of Humid Old-Growth Forests of the World

Markku Larjavaara (✉ [markku@pku.edu.cn](mailto:markku@pku.edu.cn))

Peking University <https://orcid.org/0000-0002-3484-889X>

Xiancheng Lu

Peking University

Xia Chen

Peking University

Mikko Vastaranta

University of Eastern Finland

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## Research Article

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# Abstract

**Background:** Understanding how warming temperatures are influencing biomasses in the world's forests is necessary for quantifying future global C (carbon) budgets. A temperature-driven decrease in future C stocks could dangerously strengthen climate change. Empirical methods for studying the temperature response of forests have important limitations, and modelling is needed to provide another perspective. We modelled current and future AGB (old-growth above-ground biomass) in humid lowland areas of the world by dividing GPP (gross primary productivity) and a measure of energy needed to support a given amount of biomass called here MCB (maintenance cost per unit biomass).

**Results:** Based on the modelling, we predict a temperature-driven increase in both GPP and MCB, except in the tropics, where GPP will decrease. Their ratio, and therefore also ABG, is expected to decrease in all other regions except the boreal. The AGB is expected to decrease 41% in the tropics and 29% globally.

**Conclusions:** The estimated drops in AGB are dramatic. However, we did not include the fertilisation effects of increasing CO<sub>2</sub> (carbon dioxide) and N (nitrogen) that potentially mitigate the temperature-caused drop in AGB.

## Background

Forests influence climate change by storing C (carbon) that could alternatively be held in the atmosphere as CO<sub>2</sub> (carbon dioxide)(1). However, forests are also influenced by climate change, as temperatures control tree physiology (2). If this feedback is negative and more C is stored in forests with warming air temperatures, forests mitigate climate change. If the feedback after a time lag is positive, global warming will continue despite a complete cessation of direct anthropogenic emissions. Knowledge concerning the impact of warming temperatures on forests is necessary for quantifying global warming caused by a given anthropogenic emission level.

Multiple methodologies are available to empirically study the impact of changing temperatures on forests. Perhaps the most straightforward conceptual approach is to simply document how growth or old-growth biomass has changed in recent decades and then assume the same trend to continue in the future. Canadian inventory data does not indicate a general change in trunk basal area growth (3). Similarly, height growth in Finland seems to have increased very little or not at all (4). In the Amazon rain forests, biomass growth increased in the 1990s but has since levelled off (5).

In addition to changing temperatures, changing CO<sub>2</sub> concentration, N (nitrogen) deposition and other factors, such as changing precipitation, have influenced the long-term trends in tree growth. Disentangling their impacts is possible by focusing on year-to-year variability, e.g. based on annually repeated diameter measurements, tree rings or dendrometers. Diameter growth has been faster during warmer years in northern Finland (6). In contrary, diameters grew less in lowland Costa Rica during years with warmer diurnal minimum temperatures (7). In line with these local studies a global dataset reported positive correlation between temperature and tree ring widths in northern boreal but negative in other biomes (8). Even when focusing on year-to-year growth variation, the temperature signal may be masked by covarying

meteorological variables, such as cloudiness, or by time lags e.g. if trees build reserves during good years instead of adding to their growth or if e.g. waterlogging kills deeper roots limiting growth over following years. These challenges can be avoided with long-term experiments. Warming all the tissues of large trees is practically impossible but warming of the soil in a temperate forest increased biomass growth (9), and whole-plant warming of potted tropical trees had mixed impacts on their growth (10).

Results on tree growth are valuable but insufficient to understanding the forest-warming-feedback for which stored C matters, as mortality is likely to change as well (11). For example, if mortality increases more than growth, a warming-triggered boost in growth will lead to reduced biomass. Therefore, studies reporting changes in biomasses are especially valuable. Unfortunately, most forests are typically successional, even in remote areas in biomes influenced by large-scale disturbances, such as fires, and are far from an old-growth state in which biomass can be assumed to remain unaltered without global change impacts. However, a biomass change in remote regions or tropical rain forests lacking fires can be assumed to be naturally steady-state and any change can be attributed to global change. Forests in the Amazon basin (5), equatorial Africa (12), and Borneo (13) have all been shown to increase in biomass, but as with studies regarding growth, disentangling the impact of warming temperatures from other global change drivers is difficult. Furthermore, measuring large trees is surprisingly challenging (14), and even minor inaccuracies may significantly bias subtle trends (15). An additional challenge is that a seemingly stable old-growth forests may be actually recovering e.g. from anthropogenic disturbances that occurred centuries ago or from more recent natural disturbances such as drought (16).

The above-presented empirical approaches have provided valuable views from numerous perspectives, but overall understanding unfortunately remains blurred and even the direction of global forest biomass change caused by warming is questioned. Furthermore, all these empirical approaches neglect longer time lags in future biomass change, which are important in relation to precipitation (17). For example, an increasing temperature may weaken and kill the dominant tree species adapted to colder temperatures (18) before a species adapted to the new warmer climate is able to accumulate biomass above the initial level. If the new species were already present in the forest, the transitional phase could last for decades, but would take longer if tree migration is involved. These challenges suggest that modelling may significantly improve our understanding concerning the long-term impacts of global warming on forest biomass from that based on empirical research.

Models on global biomass patterns range in the levels that they are based on physiological processes determining biomass rather than the direct statistical estimation of biomass. Direct statistical modelling is not well suited for global future biomass modelling, as some future climates are currently found nowhere on Earth (19). Models including physiological processes vary greatly in their complexity. Earth system models, which attempt to quantify all major processes in the ecosphere, are extremely complex and therefore potentially very accurate at predicting future changes. Unfortunately, they are not good at predicting current AGB (old-growth above-ground biomass) variation (15), and their complexity makes open discussion on their structure and assumptions difficult. There is clearly a substantial need to model current global AGB and apply the same approach to predicting long-term future changes with a simple physiological model.

The normal way to understand biomass based on physiological processes is grounded on the production and decay of materials (20). Based on this thinking, exceptionally high biomass can result from large production or long residence time, i.e. turnover, of the material produced, or both. The focal “material” ranges from focusing only on woody biomass (21) to all ecosystem C (22). When applied to the AGB:

$$AGB = \frac{NPP}{D}, \quad \text{Eq. 1}$$

where NPP is above-ground net primary production and D is its decay, i.e. the reciprocal of turnover. NPP can be quantified with field measurements and understood based on physiological theories. However, even though D is intuitively reasonable, it is difficult to explain physiologically or make guesses about its climate-driven variation, unlike when focusing on dead tissue that decays predictably (23). In general, D increases with decreasing size, as small trees have a smaller proportion of biomass stored in long-term pools such as trunks. However, plants vary also in how often they replace leaves and in a given climate. Deciduous trees have both higher NPP and D than evergreens, possibly resulting in the same AGB. Because of these challenges, in practice, D is obtained statistically as the quotient of NPP and AGB.

Perhaps less intuitive, but better for numerous reasons, is focusing on the input and output of energy, i.e. chemical energy in both structural and non-structural material, instead of focusing on more permanent structures only. Maintaining living biomass consumes energy. As the input of energy in the ecosystem, GPP (gross primary productivity) does not vary much during the succession after canopy closure (24), and there must be a maximum biomass that the available energy can support and that can be estimated based on GPP and maintenance cost. In this energetic approach, Eq. 1 is modified to:

$$AGB^b = \frac{GPP}{MCB}, \quad \text{Eq. 2}$$

where b is a parameter and MCB is the maintenance cost per unit biomass, not only including autotrophic respiration but also heterotrophic respiration resulting from the turnover of tree parts and mortality (25). Parameter b was added, as autotrophic respiration does not increase linearly with increasing tree size (26), and was parametrised to 0.4 with a global data set (25, 27). In practice, similarly as with D in Eq. 1, MCB is best understood as the quotient of GPP and  $AGB^b$ , and this understanding can then be used to model AGB. MCB in Eq. 2 can be understood better based on temperatures than D in Eq. 2 as it is composed in addition to the challenging heterotrophic respiration of autotrophic respiration with a well know temperature dependency (28) and data on GPP are readily available from eddy flux towers and can be modelled straightforwardly based on temperatures.

Water is crucial for trees, and many global patterns are well explained by annual precipitation (17), and its influence on AGB is certainly important (29) and probably increasing in importance (8). However, it is challenging to incorporate water into AGB modelling, as trees may obtain water from deep layers of the soil (30) and therefore even a dry climate may therefore be conducive to tree growth. Even reaching the water tables of forested regions of the world seems to be biomechanically easy compared to building massive trunks upwards that resist winds and gravity. Instead, much of the precipitation-impact on AGB could be caused by the covarying vapour-pressure deficit or even more indirectly via wildfires that increase with dryness (31), further complicating quantification of the mechanisms.

The energetic approach (Eq. 2) explained well the current global AGB variation in humid forests around the world (25, 27). As the approach is temperature driven, it is ideally suited to approximate long-term future changes in the AGB of humid forests. Our objective was to quantify changes in AGB caused by climate change in humid regions of the world based on this energetic approach and to determine the causes of these changes.

## Methods

We used historic monthly means of diurnal minimum and maximum temperature (near-surface air temperature) data from 1970–2000 of the WorldClim 2.1 data set (46). We call this climate and the resulting AGB “current” for simplicity, even though some decades have passed. Because of time lags in AGB response to temperature, we intentionally use the term “current” to express the vagueness. To study the impact of warming temperatures on ABG, we used projected temperatures for 2081–2100, which were estimated based on an ensemble of models (47) and were run based on an intermediate emission scenario SSP2-4.5 (48). Similarly, as with the “current” climate and AGB, we use the terms “future climate” and “future AGB” to refer to these predicted temperature regimes and predictions based on them. If the climate were to stabilise at this future climate, ABG would stabilise at its new level after a time lag. We used a 10-minute spatial resolution in the analysis.

Our analysis was based on the physiological models described in 2012 (25) and corrected parameter values reported in 2013 (27). We decided not to modify the models or use updated parameterisation data sets, to allow interpretation of the results based on the earlier papers and to avoid overparameterisation. In summary, GPP is primarily dependent on temperature that is assumed to cycle diurnally between the monthly mean minimum and maximum. GPP is positive between  $-5^{\circ}\text{C}$  and  $+40^{\circ}\text{C}$  and peaks at  $+25^{\circ}\text{C}$ . In addition, GPP is only possible with positive sun angles and is higher with a higher angle. Finally, a large change in temperatures from the previous month reduces GPP. AGB depends on the ratio of GPP and MCB (Eq. 1), and MCB is computed by assuming the so-called  $Q_{10}$  temperature coefficient, with a 1.67-fold MCB for an increase of  $10^{\circ}\text{C}$  (27). As with GPP, a change in temperature from the previous month causes an extra energetic expense that is proportional to the temperature difference.

We excluded arid and high areas in the same way as the study fitting the physiological models (25). We computed annual potential evapotranspiration based only on current temperatures with a classic method (49), and excluded areas where current annual precipitation was smaller than the potential

evapotranspiration based on WorldClim 2.1 (46). We excluded highlands at least 1000 m above sea level (50). However, we did not exclude oceanic islands that have never been connected to continents, as was done previously (25), but as their total area is minimal, their impact on our results are also expected to be minimal. Theoretically, our findings on oceanic islands should be viewed as indicating the potential AGB of exotic continental tree flora in the climate of each island, rather than the AGB of the local species communities.

Thanks to the simplicity of the modelling approach, we could quantify the sensitivity of our results relative to all thirteen parameters, parameter bounds, or data selection criteria that influenced either the maximum temperature at which GPP is possible or the base of 1.67 on the temperature sensitivity of MCB. We were interested in this maximum temperature and the base number, as we expected these to drastically influence how increasing temperatures are expected to affect AGB, particularly in the tropics.

## Results

In the current climate (1970–2000), GPP was estimated to be highest in the tropics (see Table 1 for definitions of latitudinal zones) and to decrease towards the poles (Fig. 1a). In the future climate (2081–2100), estimated GPP increased in all other latitudinal zones except the tropics (Table 1). However, due to the large area of humid lowland forests in the tropics, the global mean decreased slightly (Table 1). Increasing temperatures levelled the global variation in GPP, and the intermediate values expanded geographically (Fig. 1b). The 4.6-fold GPP in the tropics relative to the boreal dropped to a 3.2-fold difference.

Table 1

Four latitudinal zones, their areas, estimated GPP, MCB, AGB (old-growth above-ground biomass) and net C flux assuming that 47.6% of AGB is C (51) for the studied humid lowland forests. Current values were estimated based on the climate of 1970–2000 and future values based on a projected climate for 2081–2100.

<i>Zone (latitudes)</i>	<i>Total area (million km<sup>2</sup>)</i>	<i>Current mean GPP (kg m<sup>-2</sup> yr<sup>-1</sup>)</i>	<i>Future mean GPP (kg m<sup>-2</sup> yr<sup>-1</sup>)</i>	<i>Current mean MCB (yr<sup>-1</sup>)</i>	<i>Future mean MCB (yr<sup>-1</sup>)</i>	<i>Current mean AGB (kg m<sup>-2</sup>)</i>	<i>Future mean AGB (kg m<sup>-2</sup>)</i>	<i>Mean AGB change (kg m<sup>-2</sup>)</i>	<i>Total C change (Pg)</i>
Boreal (55° N – 90° N)	11.0	0.70	0.92	0.11	0.14	10.06	11.59	1.52	8
North temperate (23.5° N – 55° N)	15.9	1.58	1.73	0.18	0.22	22.36	18.33	-4.03	-30
Tropics (23.5° S – 23.5° N)	21.7	3.21	2.95	0.31	0.35	37.67	22.18	-15.50	-160
South (90° S – 23.5° S)	3.2	2.33	2.42	0.21	0.24	41.66	35.15	-6.51	-10
<b>World</b>	<b>51.7</b>	<b>2.13</b>	<b>2.11</b>	<b>0.22</b>	<b>0.26</b>	<b>27.37</b>	<b>19.55</b>	<b>-7.82</b>	<b>-193</b>

MCB had a similar global pattern as GPP based on the current climate (Fig. 1c). However, increasing temperatures increased MCB in all regions, and all MCB classes moved towards the poles (Fig. 1d). As with GPP, the ratio of MCB in the tropics to MCB in the boreal dropped, but only slightly, i.e. from 2.8 to 2.5.

As AGB was modelled based on the ratio of GPP to MCB (Eq. 1), and both increase towards the equator, we expected a more complex global pattern. Tropical, subtropical and temperate forests were estimated to have the highest AGBs, with a clear decreasing trend towards the North but also towards the central and eastern parts of the continents both in Eurasia and North America, which have more continental climates, i.e. more seasonal temperature variations (Fig. 1e). The highest AGBs were located in regions elevated to at least a few hundred metres above sea level in the tropics and subtropics, such as central Borneo, but also in maritime mid-latitudes such as North island of New Zealand. Interestingly, as northern temperate humid lowland forests had a more continental climate than forests in the zone south, located at a similar distance from the equator, the mean AGB for the tropics was significantly higher than for northern temperate but somewhat lower than for the south (Table 1).

The increasing temperatures led to a dramatic drop in the AGB of the tropics but an increase in the boreal (Fig. 1g). The resulting AGB pattern was more even than that based on the current climate (Fig. 1f). However, as the mean drop of 41% in AGB in the tropics is so significant relative to the modest increase of 15% in the boreal, the overall global change is strongly negative (Table 1).

The estimated decrease in humid lowland forest C from current to future was 193 Pg of C (Table 1). The drop in tropical AGB caused 83% of this global decrease. The period during which this estimated change would happen is uncertain, but assuming a century of change, the annual emission rate of  $1.93 \text{ Pg yr}^{-1}$  can be compared e.g. to an increase of  $4.9 \text{ Pg yr}^{-1}$  in atmospheric C in recent years (32).

Our results were surprisingly robust to changes in the parameters, parameter bounds or data selection criteria in the earlier study (25) that we tested (Supporting information). However, considerable variation still occurred. For example, the global AGB decrease estimated to be  $7.82 \text{ kg m}^{-2}$  actually ranged from  $5.93$  to  $10.08 \text{ kg m}^{-2}$  in the sensitivity analysis. As expected, much of this variation was caused by uncertainty in the tropics, in the future much of which will have a climate not currently found on Earth.

## Discussion

We applied a simple physiological model that previously successfully explained current global AGB variation based on monthly temperatures (25), to estimate the impacts of rising temperatures on the AGB of humid lowland forests. Our approach was based on focusing on GPP and ecosystem respiration, similarly as that of Duffy et al. (33), and they are equal by definition in a steady-state old-growth forest. However, we processed the data very differently. In a steady-state ecosystem, all dead tissue will decompose, and the timing of this decomposition within the annual cycle does not influence AGB. Instead, we divided ecosystem respiration by a power of AGB, called this MCB, and assumed it to depend on temperature.

Our aim was not to predict the impact of rising temperatures on forests to be used directly in global C balance predictions, but instead to present the results of our approach as basis for further discussions. Therefore, the simplicity of our model should be viewed as an advantage, as its pros and cons are easier to comprehend than those of more complex methods. Based on our approach, AGB decreases if the ratio of GPP to MCB decreases (Eq. 2), and MCB can be viewed as the maintenance cost of a unit mass of a given biomass type per unit of time. As both GPP and MCB are dependent on temperature, their ratio obtains its maximum at a given temperature. This temperature is  $16.4^\circ\text{C}$ , assuming no diurnal temperature variation and a given sun path (25, 27). Their ratio decreases in warmer temperatures, as MCB increases faster than GPP, while GPP decreases faster than MCB in colder temperatures. Seasonal temperature variation decreases AGB when mean annual temperature is close to this optimum, as this variation inherently shifts temperatures away from the optimum. In addition, the fitting of these physiological models included parameters that cut GPP and increase MCB proportionally to the temperature difference to the previous month due to imperfect acclimation (25).

The simple modelling approach that we used successfully predicted global AGB patterns (25, 27) but failed to explain certain more local findings. Based on our energetic principles, when nights only are considered, colder temperatures should allow more rapid growth and greater maximal size, as GPP is zero when light is not available because MCB decreases with decreasing temperature. In contrast to this, small trees have grown faster during warmer nights in an outdoor experimental setup with tropical pioneer seedlings (34). However, this should perhaps be regarded as an exception because the proportion of biomass and growth of small pioneers in full light is very small, and indeed the growth-boosting effect of warmer nights

disappeared with larger trees (10). It seems likely that warming nights enhance the growth of small seedlings if their growth is not limited by available energy but by the speed of new tissue synthesis that increases with increasing temperature or perhaps the large diurnal temperature variations is challenging for a number of biochemical processes. A second set of findings, that is difficult to explain with our energetic approach, comes from elevational gradients. Studies on elevational gradients starting from the lowlands in the tropics have revealed both decreasing and increasing biomasses towards higher elevations (15), even though when focusing only on temperatures and energetics, biomasses should peak in mean annual temperatures of approximately 10–15°C, depending on the diurnal temperature variation. This corresponds to an elevation of approximately 2 km close to the equator (35). Globally, the tallest trees have been shown to grow in this thermal climate in maritime regions in the mid-latitudes, and reasons for this potentially include the lack of huge trees in most tropical mountain ranges, but these reasons are still partially unclear (36). A third shortcoming in the energetic approach that we applied relates to its fundamental assumptions. It is not difficult to see how e.g. a patch of evergreen species has both a smaller GPP and MCB than a neighbouring patch of deciduous species with the same AGB. However, based on the relative tight fit of the GPP and MCB models (25, 27), this does not seem to cause much variation and is even less likely to cause significant bias.

Despite its limitations, our approach based on GPP and MCB is overall likely to be the optimal methodology if this level of simplicity and physiology is pursued. However, even in a hypothetical situation in which only temperatures were to change, our predictions should not be taken as estimates of AGB in 2081–2100. Most of the original field measurements according to which the physiological models were parameterised were conducted a couple decades later (37–39) than the climate data we used (40). Based on this, our current AGB is from the turn and first decades of the 21st century and our future AGB would be relevant at the beginning of the 22nd century. However, this would give an overly exact image of our predictions, as complex time lags may blur the real picture. These lags may drastically depend on whether the future dominant tree species are already dominant in the forest, are present but rare or need to migrate to the location. When species-poor communities face dramatic climatic changes, significant migration may be needed and AGB may be significantly depressed after the early mortality of the original tree population. This kind of processes may be the cause of the current increased mortality (11), if sustaining the earlier AGB is not possibly energetically.

Exact AGB predictions become even more challenging when other global change factors, such as the fertilising effect of increasing atmospheric CO<sub>2</sub> and N deposition, are also considered. It could be that the negative temperature impact and positive fertilisation impact roughly compensate each other in tropical lowland rainforests (41). However, proportionally stronger impacts should not be assumed to still balance out, as a positive impact far above the evolutionary history of the tree may not be physiologically significantly more beneficial than a smaller impact, while a negative impact below the range in evolutionary history could be disastrous. Further complications include changes in precipitation and transpiration that are challenging to forecast, and trees may be able to transpire less thanks to increasing atmospheric CO<sub>2</sub> (42), but may even transpire more to cool leaves down in certain conditions (43). Water balance may also

influence biomasses via disturbances, especially fires, which may override other mechanisms in the boreal (44).

We estimated emissions of nearly 200 Pg of C due to the warming temperatures. However, this estimation was assuming that all humid lowland area was old-growth forest, which is far from the reality. Natural disturbances, such as fires, have influenced a large proportion of area especially in the boreal, much of the area unsuitable for forest growth is covered by waterbodies or waterlogged soils, or is disturbed by humans through logging or more severely through agriculture or settlements.

Numerous avenues exist for future studies following these same principles (Eq. 2). Complexity could be increased by taking actual land uses and their changes into account and comparing to observed patterns (45), by including arid and high areas or by incorporating other mechanisms such as the CO<sub>2</sub> fertilisation effect. Alternatively, this same energetic approach (Eq. 2) can be used to understand succession unlike the more traditional way to understand AGB (Eq. 2). Temperature-based understanding of succession would open new possibilities to e.g. optimise wood production and storing C globally in both current and future climate.

## Conclusions

Based on our pioneering approach, we predict a severe drop in the AGB of tropical forests and some decrease in the AGB of temperate forests. In contrary, we expect an increase in the AGB of boreal forests, but this increase is minuscule per unit area and especially globally when multiplied by its area, when compared to decreases in the warmer regions. Our results are particularly valuable, as we estimated AGB directly. It is not uncommon to see predictions of changes in GPP and NPP with associated predictions on biomass without considering what happens to respiration.

## Declarations

### Availability of data and materials:

The study is based on datasets published earlier.

### Competing interests:

None

### Funding:

Peking University

### Authors' contributions:

M.L. developed the research idea, X.L., M.L. and M.V. modelled the impacts, and M.L., X.L. wrote the first manuscript version and all authors produced the final version.

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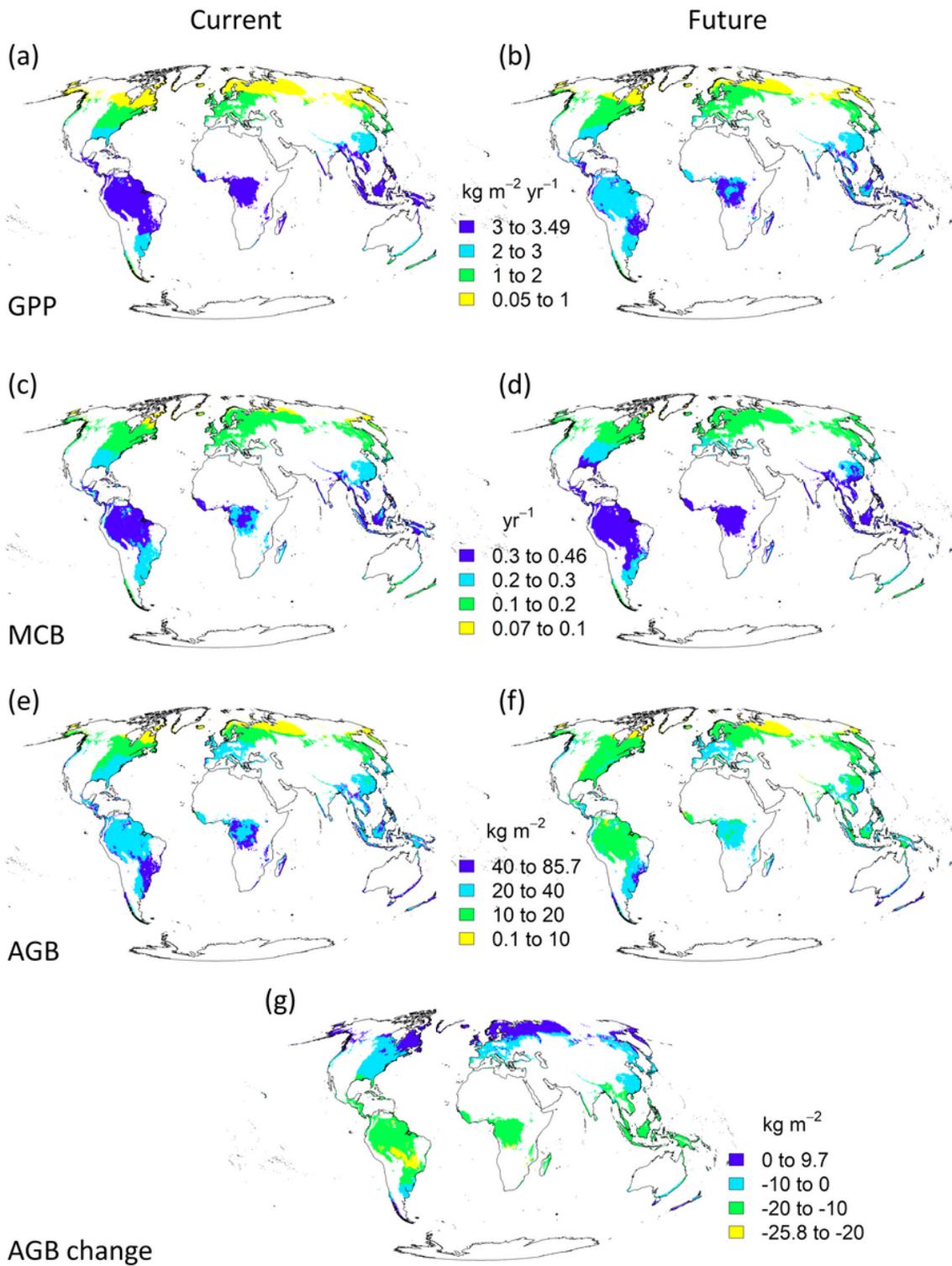
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## Figures



## Figure 1

GPP, MCB and AGB currently based on the climate of 1970–2000, and future values based on a projected climate for 2081–2100. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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