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Review

Trailblazing the Carbon Cycle of Tropical Forests from Puerto Rico

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Abstract: We review the literature that led to clarifying the role of tropical forests in the global carbon cycle from a time when they were considered sources of atmospheric carbon to the time when they were found to be atmospheric carbon sinks. This literature originates from work conducted by US Forest Service scientists in Puerto Rico and their collaborators. It involves the classification of forests by life zones, estimation of carbon density by forest type, assessing carbon storage changes with ecological succession and land use/land cover type, describing the details of the carbon cycle of forests at stand and landscape levels, assessing global land cover by forest type and the complexity of land use change in tropical regions, and assessing the ecological fluxes and storages that contribute to net carbon accumulation in tropical forests. We also review recent work that couples field inventory data, remote sensing technology such as LIDAR, and GIS analysis in order to more accurately determine the role of tropical forests in the global carbon cycle and point out new avenues of carbon research that address the responses of tropical forests to environmental change.

Keywords: biomass; allometry; volume expansion factors; soil organic carbon; tropical forest area; forest inventory data; novel forests; tree plantations; secondary forests; mature forests

1. Introduction

When Leslie Holdridge became the first scientist at the Tropical Forest Experiment Station of the USDA Forest Service in Río Piedras, Puerto Rico in 1939, no one knew that the International Institute of Tropical Forestry (as it became known in 1993) would become heavily engaged in helping unravel the role of tropical forests in the carbon cycle of the world. Based on his experience in the Caribbean, Holdridge developed the Life Zone System for identifying vegetation formations from climatic data [1,2]. Decades later, we showed that Holdridge life zones correlated with carbon storages and fluxes of mature tropical forests [3]. As a contribution to the 75th anniversary of the Institute, we review the contributions of its scientists and collaborators to the understanding of the carbon cycle of tropical forests. We also make observations about the evolving role of tropical forests in storing carbon in the context of the Anthropocene Epoch.

2. Foundational Research

Carbon-related research requires considerable background information about tropical forests such as knowledge about dendrology including wood properties and stand volume stocks. This type of information facilitates estimates of stand biomass and conversion of stand structure to biomass. Institute scientists developed some of that information during the 1950s and 1960s [4,5]. This included tree identification [6,7], the wood properties of tree species [8,9], regressions for tree volume and biomass estimation [10–13], and volume tables for timber species [14,15]. A system of long-term observation plots was also established in the early 1940s to assess tree growth and stand volume yields [14,16–18]. Some of these plots in the Luquillo Mountains, the oldest under continuous measurement in the Neotropics, are described in [19] (pp. 91–92). The tree plantation program of the Institute also yielded information about plantation wood yields under different conditions and plantation species [20].

3. Carbon Flux and Storage Studies at the Institute

During the late 1950s and early 1960s, Institute collaborators Howard T. Odum and Frank B. Golley estimated the biomass of a *Rhizophora mangle* L. forest [21] and a tabonuco (*Dacryodes excelsa* Vahl) subtropical wet forest [22–24]. Both studies were pioneering in the field of ecology and both led to ecosystem-level carbon budgets for these two types of tropical forests. The Odum studies at the Luquillo Mountains developed into the Radiation Experiment at El Verde [25], which explored in depth the carbon dynamics of a tropical forest [10]. In Figure 1 we reproduce the resulting carbon budget (expressed in energy units) for a stand of tabonuco forest at El Verde. This analysis stimulated similar work in other tropical forests in Puerto Rico, such as the carbon budgets for a dry forest [26–28] (see Figure 7.8 in [28]), a palm floodplain forest (see Figure 8 in [29]), various tree plantation species [30,31], and for tree plantations and secondary forests of similar age [32]. In Brazil, Institute scientist Michael Keller and collaborators addressed the carbon cycle of Amazonian forests through allometry [33,34], remote sensing and LIDAR [35], and detailed studies of the effects of logging on the carbon cycle and coarse woody debris (necromass) dynamics [36–38]. More recently, Institute scientists addressed the carbon dynamics of novel forests. Novel forests are secondary forests growing on deforested and degraded lands, and are dominated by naturalized tree species [39–44]. These forests behaved as net carbon sinks.

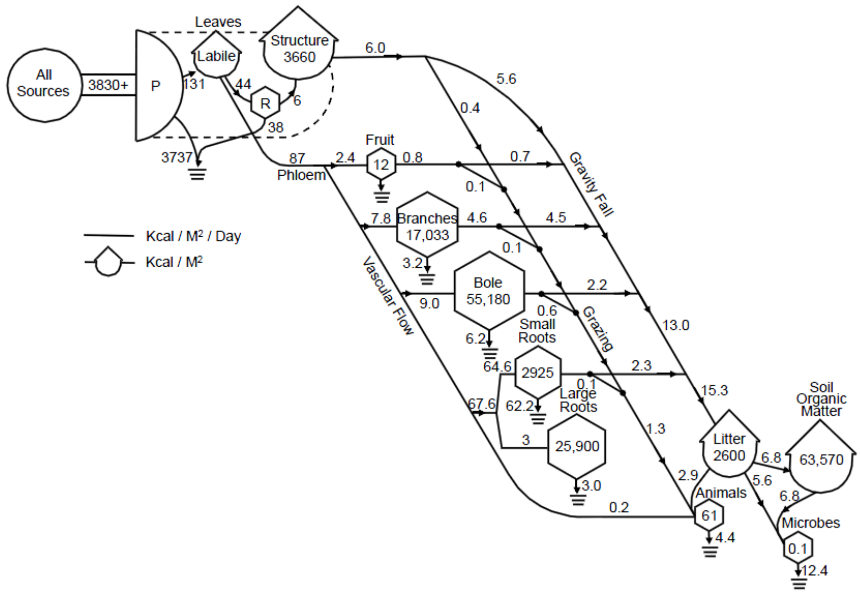

Figure 1. Carbon budget of a subtropical wet forest at El Verde, Puerto Rico [10] expressed in energy units (about 4 kcalories per g of vegetation material, because Odum used caloric equivalents of the various materials). The budget was constructed assuming steady state for the whole system. However, plants do exhibit greater production than respiration. Photosynthesis is P, R is respiration, structure refers to leaf biomass, and the symbols are those of the energy language of Odum [10]: bullet symbol represents photosynthesis, hexagons are consumer compartments, tanks are storages, the circle represents external energy inputs, the heat sinks are energy losses as a result of energy transformations, and lines represent the fluxes.

The above studies resulted in a number of insights about the carbon dynamics of tropical forests, many of which still hold or apply under comparable conditions. For example:

- ➢ A large fraction of the carbon uptake in mature forests is consumed by stand respiration, with low net yields [10]. This result confirms early research that showed slow tree growth and low volume yields in these forests [4,15].
- ➢ Large pools of carbon and nutrients in these forests tend to be belowground (mostly in soil), contrary to early beliefs that tropical forests stored most of their nutrients and mass aboveground [45].
- ➢ Stand biomass of mature forest varies as much as five-fold depending on topographic position on the landscape [11].
- ➢ Root biomass tends to be higher in mature forests compared to successional ones and higher in native forests compared to timber tree plantations of similar age [32].
- ➢ Forested watershed export of carbon is proportional to runoff [29,46,47]. The export of organic matter from a floodplain forest at high elevation is high (35 $g/m^2 \cdot year$; [29]) compared to forested tropical watersheds at lower elevations (2.2 to 15.5 $g/m^2 \cdot year$). Forested watersheds in turn exhibit higher organic matter exports than intensively used watersheds (weighted average of 3.7 $g/m^2 \cdot year$ (range of 1.5 to 10.5 $g/m^2 \cdot year$) for 14 intensively used watersheds) [47].
- ➢ Secondary and novel forests accumulate aboveground biomass and nutrients at high rates, and circulate a large fraction of their net primary productivity to the forest floor [41,48,49]. Novel forests have a higher rate of litterfall and nutrient return to the forest floor than native forests in similar climates and soils [39–43].
- ➢ Wood density increases with age and maturity of forest stands. For example, stand-weighted specific wood density increased by 3.9% (from 304 Kg C/m^3 to 316 Kg C/m^3) among dichotyledon trees in mature *Cyrilla racemiflora* L. forests over a 35-year period in the Luquillo Mountains [50].
- ➢ Logging can be an atmospheric carbon source and its carbon effects can be mitigated, but not eliminated, through management such as reduced impact logging [36].

4. Estimating the Global Role of Tropical Forests in the Carbon Cycle

The carbon budget of tropical forests gained increased scientific attention when Woodwell et al. asserted that "analysis shows through convergent lines of evidence that the biota is not a sink and may be a source of CO_2 as large as or larger than the fossil fuel [51] (p. 141)." They estimated that the biota was a global source of carbon of up to 8 Pg/year. This statement and analysis was controversial because it undermined the prevailing understanding of the global carbon cycle, as scientists could not anticipate how the atmosphere and oceans could absorb such a high level of carbon input [52] (Table 1). Research was needed to improve the understanding of the carbon budgets of tropical forests and decrease the uncertainty of global estimates of carbon fluxes.

The summary of forest biome biomass density of Whitaker and Likens [53] was the state of understanding of biomass distribution around the world, later updated by Ajtay et al. [54]. We argued that the types of tropical forests, and therefore their biomass density, were more diverse than the two entries used by those authors (see Table 1 in [53] and Table 5.2 in [54]). To test our hypothesis, we used a Holdridge life zone approach for assessing the biomass of tropical forests [3]. We did an intensive search of the literature on tropical forests and collected all the biomass data we located and then used the ratio of mean annual temperature to mean annual precipitation (T/P) as a surrogate of the potential evapotranspiration to precipitation ratio in the life zone chart to determine if any patterns existed between these variables. These ratios are indicators of the potential water availability to forests. We found that the T/P ratio correlated with forest and soil carbon storage (Figure 2). Using estimates of global distributions of life zones, we developed a new estimate of 185 Mg C/ha for moist tropical forests. Our estimate was lower than the values used in carbon models based on Whittaker and Likens [53] and Ajtay et al. [54]. A lower forest biomass implied lower carbon release to the atmosphere as a result of deforestation, fire, and decomposition.

Table 1. Consensus on the magnitude of atmospheric global carbon source and sink fluxes (Pg/year) at four historic moments. The perceived role of vegetation as a carbon sink and the level of uncertainty in the budget estimate are highlighted (rows in bold). Values are based on [55–57].

Global Process and Sinks	1980	1980–1989	1990–1999	2000–2007
		Sources		
Fossil fuel burning and cement manufacture	4.5–5.9	5.4 ± 0.5	6.5 ± 0.4	7.6 ± 0.4
Change in land use *	1.8–3.3	1.6 ± 1.0	1.5 ± 0.7	1.1 ± 0.7
Total	6.3–9.2	7.0	8.0 ± 0.8	8.7 ± 0.8
		Sinks		
Atmosphere	2.3–2.7	3.4 ± 0.2	3.2 ± 0.1	4.1 ± 0.1
Oceans	1.5–2.5	2.0 ± 0.8	2.2 ± 0.4	2.3 ± 0.4
Terrestrial vegetation			**2.5 ± 0.4**	**2.3 ± 0.5**
Total	3.8–5.2	5.4	7.9 ± 0.6	8.7 ± 0.7
Residual (uncertainty)	**1.1–6.8**	**1.6 ± 1.4**	**0.1 ± 1.0**	**0.0 ± 1.0**

* Estimated at 8 Pg/year by [51].

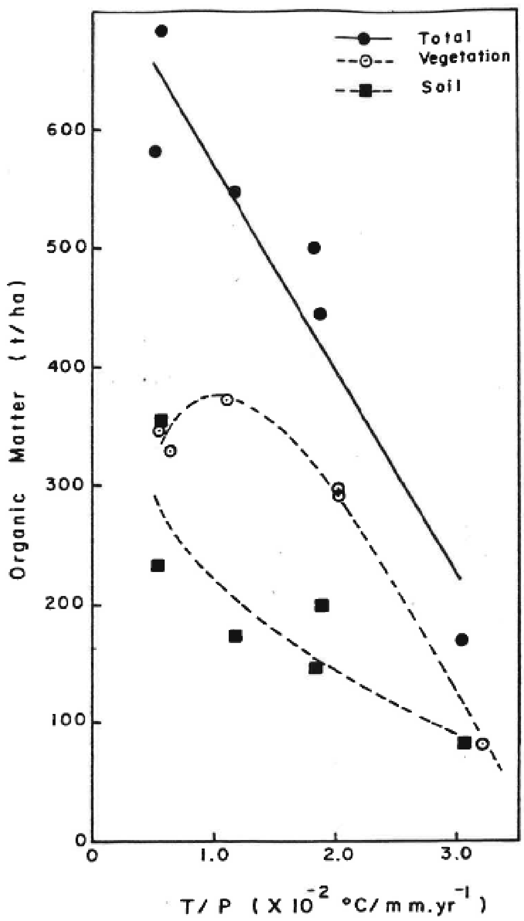

Figure 2. Relationship between aboveground and soil organic matter of mature tropical forests and the ratio of mean annual temperature to mean annual precipitation (T/P) [3].

However, we soon realized that we were synthetizing ecological information that was poorly representative of tropical forests worldwide. The ecological literature usually focused on mature forests on a few sites. For example, the database that we used for that first biomass density estimate was based on field measurements of plots covering less than 30 ha of forest cover, mostly of moist tropical forests. A larger and more representative sample size was required for a more accurate and realistic estimate of the biomass density of tropical forests. We visited the Headquarters of the Food and Agriculture Organization (FAO) in Rome, and found unpublished reports of extensive timber cruises throughout the tropical world, including the Amazon. Using knowledge from volume and biomass studies from Puerto Rico and elsewhere, we converted volume data to biomass [58]. This analysis required developing volume expansion factors for tropical forests that turned out to be different from those used in temperate regions [59,60] (Figure 3). We also developed regression equations and procedures for estimating tropical tree biomass under different life zone conditions and with different starting tree inventory information [60–62], and procedures for converting truncated volume tables to biomass estimates [63]. For root biomass, we conducted a comparative global analysis and found that root biomass density was best correlated with aboveground biomass density regardless of latitudinal location [64].

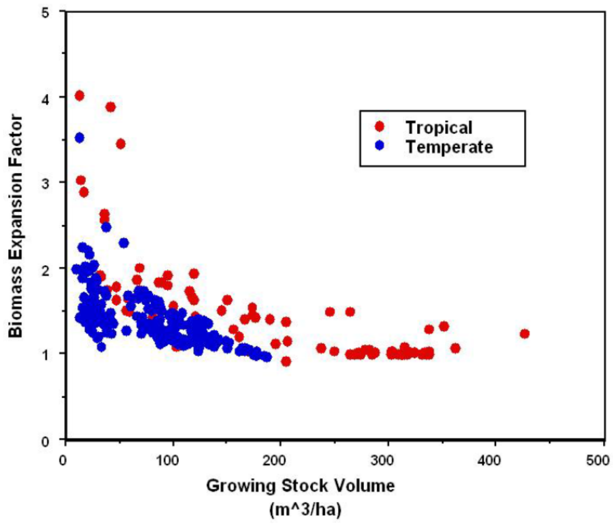

Figure 3. Relationship between the biomass expansion factor and growing stock volume of tropical and temperate forests [59,60].

Our best estimate of carbon density for closed tropical forests around the globe (99 Mg C/ha) was lower than the one based on mature forest data [59]. We deemed these forestry data more indicative of the actual biomass of tropical forests than ecological data because of the larger sample area of the timber cruises and because these volume studies were designed to estimate the actual wood volume on the landscape for economic harvests. Ecological data focused mostly on mature forest stands of limited areal extent. Decades later, when the biomass of island-wide forests in Puerto Rico was estimated from inventory data by Brandeis and Suárez Rozo [13], aboveground biomass was found to be a function of forest structure and age of stands, with the highest values in mature forests, which had the lowest area coverage.

During this stage of our work, we also focused on the carbon storage in tropical timber tree plantations and soils. For plantations, we determined both carbon storage and production rates [65,66]. For soils, our research included soil carbon content of forests and timber tree plantations [67–70], soil carbon storage in agricultural soils [71,72], and soil carbon under a variety of land covers and through succession [73–75].

Some of the insights gained about the carbon dynamics of tropical forests from the studies described in this section are listed below. Subsequent research has expanded the database, the range of values for carbon budget parameters, and addressed the carbon budget in greater detail. However, the general tendencies continue to apply:

- In mature tropical forests, carbon storage above and belowground was negatively correlated with the T/P ratio, (i.e., lower at drier locations (Figure 2)). Aboveground carbon storage peaked in moist tropical and subtropical forests and decreased towards the wet, rain, and dry forests, with dry forests exhibiting the lowest carbon density. Soil carbon storage was higher in wet and rain forests and declined towards dry forests.
- While deforestation and subsequent agricultural land use caused reductions in soil organic carbon, land abandonment and plant succession accumulated soil organic carbon at rates of 0.3 to 0.5 Mg/ha·year over 40 to 100 years [71,76]. Past land use, life zone, and stage of succession influenced soil organic carbon accumulation with higher values in older and more structurally developed moist secondary forests [67].
- Conversion of forests to pasture caused very small or negligible changes in the carbon content of the soil to a meter depth [73–75].
- Soil carbon and nutrient retention was resilient following agricultural activity [71,72].
- Succession from pasture to forests was associated with reductions in pasture derived soil organic carbon (−0.4 Mg/ha·year) and increases in forest derived soil organic carbon of 0.9 Mg/ha·year with a net increase in soil carbon of 33 Mg/ha over 61 years [70].
- Litterfall rate peaked in the moist forests and declined towards the wet, rain, and dry forests [3].
- Rate of carbon storage in secondary forests is a function of age, peaking at about 20 years depending on the life zone [74].
- Functional attributes related to organic matter production and circulation such as net primary productivity and leaf litterfall were up to ten times faster in secondary forests compared to mature forests [48].
- Large trees, defined as those with a diameter at breast height equal or greater than 70 cm, contributed few stems, generally no more than 3% of stand tree density, but can account for more than 40% of the aboveground biomass. Total aboveground biomass of stands generally increased with increasing number of large trees. These results were first reported for the Brazilian Amazon [77] but were also found to be true for Southeast Asia [78], and southeastern United States [79]. Because of their longevity, big trees collectively operate as a large and slow carbon sink in forests.
- The removal of large trees by legal or illicit felling lowers the biomass of stands and stimulates the growth of remaining trees for a limited period. This degradation process transforms mature forests into short-term successional forests with changes in rates of carbon sequestration without canopy opening. Any increase in carbon sequestration of residual trees, usually of a limited time period [80], does not make up for the loss of the felling of the large diameter trees. The assumption that closed forests are mature forests in carbon steady state is invalidated when those stands are experiencing net growth as a result of recovery from past disturbances [78].
- As stands age and larger trees develop, their rate of carbon accumulation through succession can be larger than when they were younger [70].
- Secondary forests accelerate the carbon cycle of tropical forests by turning over as much as 100 Mg/ha of biomass in a decade [48].
- Tree plantations also function as strong carbon sinks both above and belowground [81]. Their global role has changed as a result of the dramatic increase in their area since 1980 (from about 10 million hectares to 81.6 million hectares in 2015 [82]).
- Disturbances such as hurricanes accelerate the carbon cycle even more in secondary forests [83]. Hurricanes can also generate carbon sinks because initial biomass regeneration after the event can be faster than the decomposition of downed woody debris and burial of organic matter associated with landslides [84].

- ➢ Although aboveground biomass of forests can quickly recover from mechanical disturbances such as hurricanes and tree harvesting [85,86] recovery after physiological stressors such as ionizing radiation or soil degradation slow down biomass recovery rates [86–88].
- ➢ Coarse woody debris (necromass) production in Amazon intact and logged forests can account for 14% to 19% of the forests' annual carbon flux. The residence time of this necromass is 4.2 year. However, the amount of necromass in the carbon cycle of a forest cannot be accurately estimated from tree mortality data [38].

5. Tropical Forests: Carbon Sources or Sinks?

As we advanced our understanding of the carbon cycle of tropical forests, we focused attention on the question of whether tropical forests were sources or sinks of atmospheric carbon. We had already found that the biomass density of tropical forests was lower than initially thought and that maturing secondary forests dramatically increased the rate of carbon sequestration. Although with newer studies we are finding that many forests under timber concessions in Indonesia, Central Africa, and Guyana have very high biomass density before logging commences, up to 250 Mg C/ha or more [80]. We had also found that tropical soils could be important carbon sinks, particularly after abandonment of agricultural lands and through pasture or forest succession. We found that even at maturity tropical forests continued to accumulate carbon in the growth of developing large trees, increasing the weighted wood density, accumulating soil carbon and aboveground biomass (including necromass), and exporting organic carbon. The leaching of organic carbon from mature forests is a slow atmospheric carbon sink that is exported downstream from the terrestrial sector of the biosphere. Thus, to address the question of carbon balance, we needed information on land cover and land cover change to expand our findings on carbon dynamics of stands to larger scales.

While browsing in the stacks of the Commerce Department Library in Washington, DC, we ran across the two-volume analysis of the global forest resource by Zon and Sparhawk [89]. This work, commissioned for the first global Forestry Congress in the United States, gave us an insight about the perceived area of tropical forest in the world (Figure 4). It appeared that estimates of the area of tropical forests since the time of Zon and Sparhawk had shown an increase. Moreover, recent estimates are similar to estimates in the 1970s, which considering the inaccuracies of such global estimates, suggested little change in actual forest area. It was possible that global carbon models were using rates of tropical forest deforestation that were much higher than perception from a number of estimates conducted by different organizations. At the time of the Woodwell et al. paper [60], estimates of annual tropical deforestation ranged from 2% to 4%. Higher deforestation rates, multiplied by higher estimates of biomass density of tropical forests would yield higher carbon emissions to the atmosphere than would the use of our lower estimates of biomass density and lower rates of deforestation (1% per year or less).

Moreover, the dynamics of land use in the tropics are more complex than the dynamics used by global carbon models of the time [48]. Global models typically included three states for tropical forests: mature, undergoing deforestation, and recovering from deforestation [55]. For convenience, mature forests were assumed to be in carbon steady state, and thus neutral with respect to their effects on the carbon content of the atmosphere. This fraction of the tropical forest "biome" had the largest land area assigned in the model. Thus, the global role of tropical forests in the carbon cycle was limited to those forestlands in transition since the pre-industrial atmosphere in 1860 (i.e., forestlands were either being deforested or recovering from deforestation since 1860). Models allowed 120 years for forests to reach maturity or carbon steady state with the atmosphere.

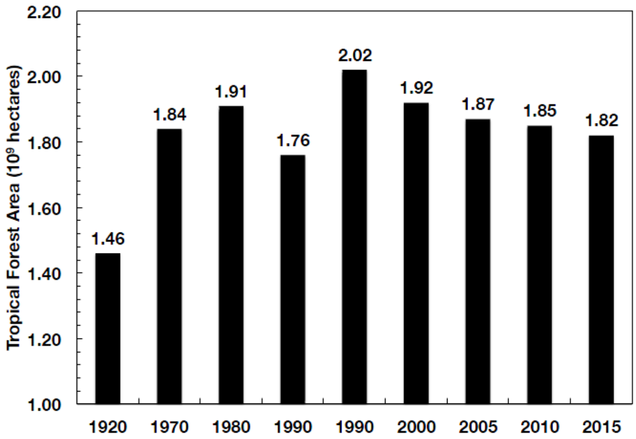

Figure 4. Area of tropical forests between the 1920s [89] and 2015 [3,82,90,91]. The 1990 estimates are both from the Food and Agriculture Organization (FAO), but estimated at different times; the last five estimates are from 2015. We selected these estimates as the most credible for their time because they contained supporting empiric information. Nevertheless, each estimate has unique assumptions and definitions that preclude precise comparisons among them.

Our analysis of the role of tropical forests on the global carbon cycle revealed that the area of forests contributing to net carbon exchange with the atmosphere was much greater than in the carbon models because the role of secondary forests was underrepresented and the carbon budget of presumed mature tropical forests was not necessarily in steady state as assumed. Moreover, we inferred from tropical forest succession literature that 120 years was too short a span of time for achieving carbon steady state. More time is needed to develop a forest structure with large trees and soil carbon at steady state [92]. Our empirical support for our arguments was summarized above and as early as 1980, when we proposed that tropical forests were sinks of atmospheric carbon [93–95]. As more information became available, we updated our case for considering tropical forests as net carbon sinks [92,96–100]. By 1992 and 1993, a shift in scientific consensus was signaled by two international conferences that were dedicated to the identification of carbon sinks in the terrestrial biota [101,102]

Today, there is general agreement that tropical forests are sinks of atmospheric carbon due to secondary forests that are predominant in the tropical landscape [103], as we had suggested many years ago [48]. Moreover, intact old-growth forests have also been shown to be carbon sinks [104], as was demonstrated in Africa [105] and confirmed in the Amazon [106,107]. However, Clark [108], questioned the analysis of plot data, and disputed this conclusion that was based on Phillips et al. [109]. Subsequently, Espírito Santo et al. [106] accounted for the effects of disturbances at various scales, and found that these sources of atmospheric carbon were smaller than the atmospheric sink functions in those mature forests, thus supporting the notion that mature forests in the Amazon were sinks of atmospheric carbon.

Table 1 shows that the 2007 magnitude of carbon sinks in the atmosphere and oceans remain within the range recognized in the 1970s but that the role of vegetation (particularly in the tropics) changed from a source to a sink of carbon, suggesting that the early models underestimated the functioning of tropical forests. The result has been that while more fossil fuel carbon is added to the global carbon cycle, the uncertainty of the global carbon budget has declined, although one can argue about the precision of those estimates. Nevertheless, increased scientific attention to the global carbon cycle has yielded better estimates of carbon fluxes and storages and highlighted additional smaller carbon fluxes that contribute to the source-sink question. An example is carbon burial [110]. According to McLeod et al., carbon burial in tropical forests is 0.04 Mg C·ha^{-1} year^{-1}, that when added to other smaller fluxes such as carbon exports from the terrestrial biota, accumulation of dead woody debris (necromass), increases in wood carbon density, carbon accumulation in large trees, soil carbon sequestration through succession, or carbon in wood products, collectively make a global difference and which we estimated as 3.1 Pg C/year in the 1990s [99].

With the onset of the Anthropocene Epoch, many worry that the sink function of tropical forests might come to an end due to changes in the atmosphere, climate change, and land cover changes [111–118]. Recent studies focus on the potential effects on the carbon balance of land degradation [119], lianas [120] residence time of woody biomass [121], stem mortality [122], selective logging [123] as well as the ecophysiological responses of tropical trees and forests to environmental change [124–129]. Clearly, there are many factors that potentially can change the carbon balance of tropical forests and convert them from sinks to sources of atmospheric carbon. However, just as forests adapted to human activity during the Holocene, they are likely to adapt to Anthropocene conditions through novelty [130]. The emergence of novel forests [131] and Anthromes [132] suggests that a major restructuring of the biota is underway and that these changes are adaptive and unlikely to fundamentally change the functioning of ecosystems. We expect novel ecosystems to adapt to Anthropocene conditions and continue to function as carbon sinks in a new world order where the speed of ecological processes is accelerated.

6. Outlook

Most aspects of our early work have been addressed recently and improved considerably in terms of geographic and ecological coverage and detail of analyses. Some examples include tree allometry [133–136], measurements of net primary productivity [137,138], the relationship between above and belowground biomass allocation [139], and the effects of hyperdominance in carbon cycling [140]. The use of permanent plots to assess carbon dynamics is now common in the literature (e.g., [141–143]). Comprehensive estimates of carbon stocks within countries (e.g., [144–146]) or across various landscape gradients (e.g., [147–150]) are also common in the literature.

New technology allows for a stronger empirical basis for estimating the global role of tropical forests. For example, our life zone approach has been expanded to encompass larger data sets and diverse controls on biomass accumulation other than climatic. These new efforts lead to cross latitudinal comparisons of the carbon cycle of forests [151,152]. We applied remote sensing and GIS technology to detect changes of carbon density of southeast Asian forests even in the absence of changes of forest cover [153–155]. The changes in biomass were due to either maturation of forests (gains of biomass) or degradation of forest stands (loss of biomass). Losses in carbon density were correlated with the perimeter to area (P/A) ratio of forest fragments, suggesting that human access was a causal factor of forest degradation. Fragmented forests ($P/A > 0$) had net biomass decreases while non-fragmented forests ($P/A < 0$) had net biomass increases. We also applied remote sensing technologies to estimate forest biomass using regressions of tree canopy area to tree carbon storage obtained from intensive fieldwork [156].

Recent field approaches for assessing carbon stocks of extensive tropical forest landscapes were also developed to assure the estimation of error of field carbon stock determinations (e.g., [157]) and expand the area covered by estimates (e.g., [158–161]). These inventory techniques using thousands of plots, coupled with high-resolution remote sensing images, LIDAR, and GIS analysis were used to conduct carbon accounting procedures for producing maps of carbon stocks and carbon emissions at various geographical scales [162,163]. Producing continental [153,164] and global [165,166] carbon density maps based on site-specific empirical information is now possible (Figure 5) in spite of the challenges involved in the development of these maps [167]. Airborne observatories such as the Carnegie Airborne Observatory [168] are shedding new light on the complexities of tropical forest cover, logging, deforestation, and climate change. These complexities of land use and cover change due to human activities can shift the carbon balance of whole landscapes and lead to new cycles of trailblazing research activity much like what happened between the 1940s and 1990s when we and other Institute scientists and collaborators had the opportunity to address similar questions but starting from a different perspective.

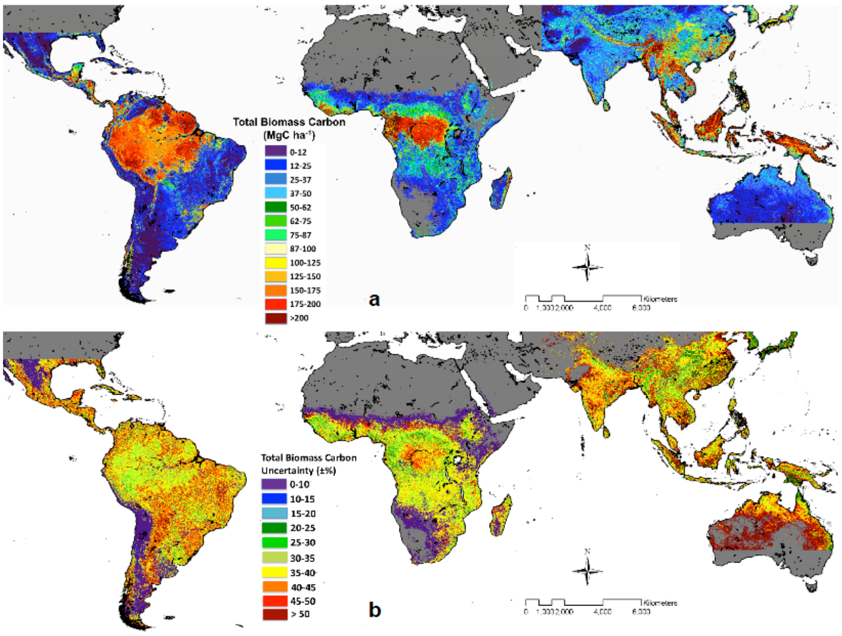

Figure 5. A global map of carbon density of tropical and subtropical forests (**a**) and the geographic distribution of the uncertainty of the estimate (**b**) [165].

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