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ESSAY REVIEW

The productivity, metabolism and carbon cycle of tropical forest vegetation

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Summary

1. Tropical forests account for one-third of the total metabolic activity of the Earth's land surface. Hence, understanding the controls on tropical forest photosynthesis and respiration, and the allocation of the products of photosynthesis to canopy, woody tissue and rhizosphere, is important to understand global ecosystem functioning.
2. I review how studies in tropical ecosystem ecology have progressed since their inception in the 1960s towards developing a quantitative, mechanistic and global description of the carbon cycle of tropical vegetation.
3. I present a synthesis of studies in tropical forest sites in the Americas and Asia for which gross primary productivity (GPP) has been reported, and a subset of these sites for which net primary productivity (NPP) and ecosystem carbon use efficiency (CUE) have been estimated. GPP ranges between 30 and 40 Mg C ha⁻¹ year⁻¹ in lowland moist tropical forests and declines with elevation. CUE in tropical forests is at the low end of the global range reported for forests.
4. A pathway and framework are presented to explain the link between photosynthesis and tropical forest biomass, and to explain differences in carbon cycling and biomass between forests. Variation in CUE and allocation of NPP can be as important as variation in GPP in explaining differences in tropical forest growth rates between sites.
5. Finally, I explore some of the key questions surrounding the functioning and future of tropical forests in the rapidly changing conditions of the early Anthropocene.
6. *Synthesis.* There have been significant recent advances in quantifying the carbon cycle of tropical forests, but our understanding of causes of variation amongst forests is still poor. Moreover, we should expect all tropical forests in the 21st century, whether intact or disturbed, to be undergoing rapid change in function and composition; the key challenge for tropical ecosystem ecologists is to determine and understand the major and most fundamental aspects of this change.

Key-words: Anthropocene, carbon use efficiency, ecophysiology, ecosystem ecology, eddy covariance, global change, gross primary productivity, net primary productivity, photosynthesis, tropical ecology

Introduction

Since the days of earliest European scientific expeditions, scientists and naturalists have remarked on, and been inspired by, the productivity, diversity and abundance of the tropical forest regions. To Europeans arriving from the wintry climes of Europe in the Little Ice Age (16–19th Century), the wet tropics provided a vision of nature set free from the restrictions of cold and drought (Bates 1864). This impression of the bountiful tropics was later muted by the realization of an apparent

contradiction: that the high productivity and biodiversity of the tropics were often based on very infertile soils. These soils are infertile due to their ancient status, not having undergone glacial weathering or benefitted from post-glacial deposition; and rapid leaching due to high rainfall and temperature.

Attempts to quantify the productivity of tropical forests began in the early 20th century, when colonial-era foresters first took an interest in managing timber yields from these forests (albeit with an inevitable focus on commercial species). These early studies focussed on wood productivity of commercial species as the most apparent and economically important aspect of tropical forest productivity. A more holistic and

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ecology-focussed approach to carbon and nutrient cycling in forests began with the emergence of ecosystem ecology as a distinct branch of ecology, with the ecosystem as a primary focus of attention (Tansley 1935; Hagen 1992). Ecosystem ecology focusses on quantifying physical flows of energy and matter (water, carbon and nutrients) through ecosystems, and on the role that physiological processes play in the development and persistence of ecosystems. Challenging research in the tropics was boosted by the advent of the International Biological Programme (IBP), with a stated objective of determining 'the biological basis of productivity and human welfare'. Tropical forest ecosystem ecology particularly advanced in the late 1960s, when the pioneer of this field, Howard T. Odum, attempted the first detailed description of large-scale ecosystem processes at the Luquillo Experimental Forest in Puerto Rico (Odum & Pigeon 1970; Jordan 1971), with the (in retrospect) rather unorthodox approach of killing an area of forest by dousing it with gamma rays (!).

The next major location for tropical ecosystem ecology was Pasoh Forest in Peninsular Malaysia, where the IBP supported efforts at measuring tropical productivity by a predominantly Japanese team (Kira 1978). The work demonstrated that it was possible (and provided the detail required) to quantify productivity through the measurement of the components of net primary productivity (NPP) and autotrophic respiration. These approaches for studying ecosystem carbon flows were 'bottom-up' in that they required the measurement of individual components of productivity, respiration and photosynthesis, often on individual plants. The key challenge, and one which still haunts current-day efforts, was one of scale: how to scale up from measurements of individual components on individual trees, to the properties of the forest stand? These attempts were also challenged by the technology of the 1970s, when technology for the measurement of carbon dioxide in the field was in its infancy.

The challenge of scale began to be tackled from a completely different direction, and by a rather different scientific community, in the 1980s, with the development of micrometeorological approaches to measure the flow of carbon dioxide between the forest canopy and the atmosphere. Micrometeorological approaches to energy and water budgets had been around since the 1960s, but the advent of field-portable fast-response CO₂ analysers and fast-response sonic anemometers enabled the advent of eddy covariance techniques, where the turbulent transfer of energy, CO₂ and other trace gases could be directly measured. For the first time, the bulk ecosystem fluxes between the vegetation and the atmosphere could be quantified with a 'top-down' approach. Such techniques measured the net flow of carbon between the forests and the atmosphere, a combination of plant photosynthesis, autotrophic (plant) respiration and heterotrophic (predominantly fungal and microbial) respiration. The net flow of carbon was termed the net ecosystem exchange (NEE) or net ecosystem productivity. Measurement of the NEE was the primary driver of these efforts, in an attempt to assess whether old-growth tropical forests were in equilibrium with the atmosphere or in disequilibrium because of global atmospheric change or past disturbance. Such

attempts at quantifying NEE have generally proved frustrating in the tropical forest environment, where there is a tendency for night-time respiration to be underestimated as cool, carbon dioxide-rich air tends to pool and flow laterally in the below-canopy air space (Finnigan *et al.* 2003; Araujo *et al.* 2008). This problem is particularly acute in tropical forest environments because the below-canopy space is large, nocturnal wind speeds tend to be low and bulk respiration fluxes are large (hence small proportional errors in respiration become large absolute errors in net carbon balance). However, the flux measurements also prove useful in quantifying the gross primary productivity (GPP, i.e. total canopy photosynthesis) of tropical forests. This can be achieved by estimating how the ecosystem respiration fluxes vary through the day based on night-time respiration measurements and then subtracting the estimated ecosystem respiration from the NEE (Reichstein *et al.* 2005).

The first reported tropical forest eddy covariance study was a short campaign in the late 1980s at the Ducke Forest near Manaus, Brazil (Fan *et al.* 1990). Such studies proliferated and expanded in duration in the 1990s and 2000s, notably in Brazilian Amazonia (Grace *et al.* 1995; Malhi *et al.* 1998) followed by a major expansion under the Brazil-led Large-Scale Biosphere-Atmosphere Project in Amazonia (Araujo *et al.* 2002; Carswell *et al.* 2002; Miller *et al.* 2004) and also in French Guiana (Bonal *et al.* 2008) and Costa Rica (Loescher *et al.* 2003). In the 2000s, they also spread into tropical Asia, in Malaysia (Kosugi *et al.* 2008), Thailand, Indonesia (Hirano *et al.* 2007) and the southern tropical fringe of China (Tan *et al.* 2010).

The flux-based approaches have been able to give insights into how productivity and metabolism are affected by variation in light, temperature and moisture availability, at scales ranging from minutes to years. On their own, however, they are unable to tease apart the internal components and mechanics of the forest carbon cycle. To do this, it is necessary to stay with the 'bottom-up' approach pioneered by Odum, Kira and others, but this time utilizing the more advanced and field-ready gas exchange technology that is now available, and possibly combining these approaches with new tools such as isotopic fractionation and DNA studies of soil microbial populations. Such an approach is able to provide a more comprehensive picture of the carbon cycle and dynamics of tropical forests (Chambers *et al.* 2004; Malhi *et al.* 2009b; Tan *et al.* 2010) to answer some long-standing questions and pose some new ones. An example of such a comprehensive picture is given in Fig. 1, for a site in Brazilian Amazonia. Currently I am coordinating a major effort to expand such work across the tropics, with sites in the wet and dry forests of Amazonia, along an elevation transect in the Andes, in forests in West and Central Africa and in Borneo, with an explicit aim of collecting data from sufficient sites to tease apart the variation of tropical forest functioning along environmental gradients (rainfall, elevation, soil type) within the tropical forest zone.

Today, tropical ecosystem ecology (and ecosystem ecology in general) forms a bridge between the realm it has traditionally occupied, that of being a branch of ecology focussed on understanding the detailed functioning and

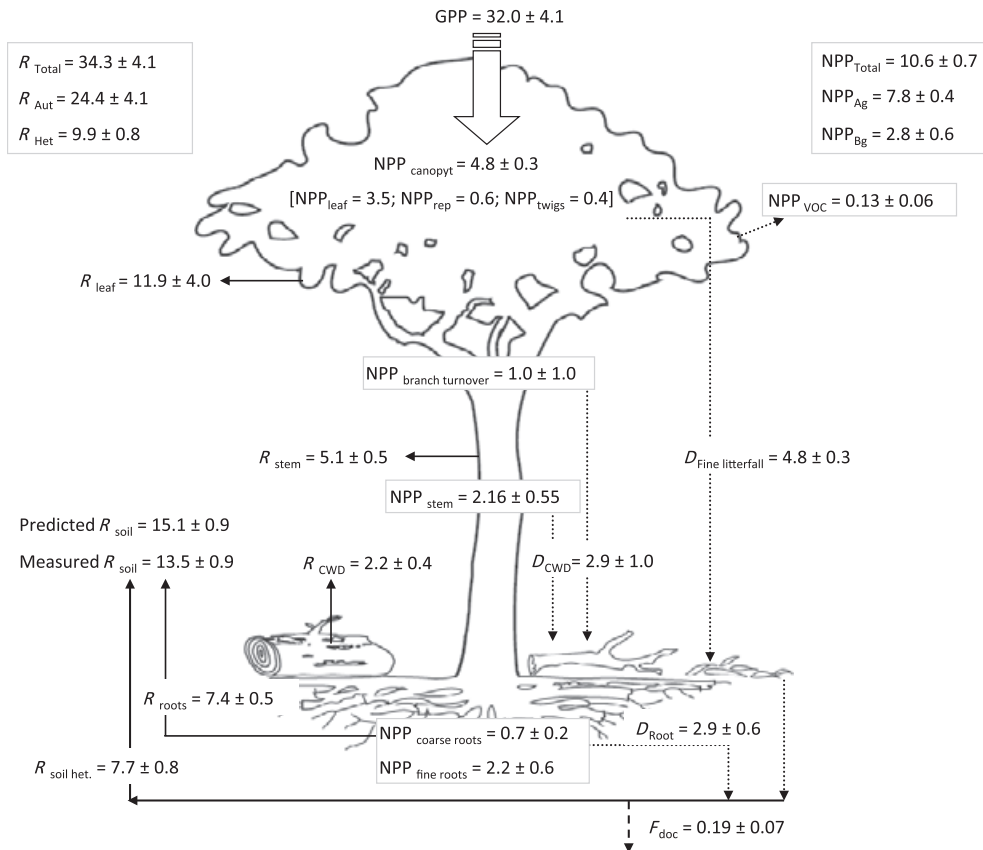


Fig. 1. An example of the full carbon cycle for a mature tropical forest in Amazonia (Caxiuanã, Brazil). Based on data from Malhi *et al.* (2009a,b), with updated values of canopy and branchfall NPP (A.C.L. da Costa, L.E.O. Aragão, D. Metcalfe, C.E. Doughty & Y. Malhi, unpublished data). GPP, gross primary productivity; R_{Total} , total ecosystem respiration; R_{Aut} , autotrophic respiration; R_{Het} , heterotrophic respiration; $\text{NPP}_{\text{Total}}$, total net primary productivity (NPP); NPP_{Ag} , above-ground NPP; NPP_{Bg} , below-ground NPP; $\text{NPP}_{\text{canopy}}$, canopy NPP; NPP_{leaf} , leaf NPP; NPP_{rep} , reproductive NPP; $\text{NPP}_{\text{twigs}}$, twig NPP; NPP_{VOC} , volatile organic compound NPP; $\text{NPP}_{\text{branch turnover}}$, branch turnover NPP; NPP_{stem} , above-ground stem wood NPP; $\text{NPP}_{\text{coarse roots}}$, coarse root NPP; $\text{NPP}_{\text{fine roots}}$, fine root NPP; $D_{\text{fine litterfall}}$, canopy litterfall; D_{CWD} , woody mortality; D_{Root} , fine root detritus; F_{DOC} , outflow of dissolved organic carbon; $R_{\text{soil het}}$, soil heterotrophic respiration; R_{roots} , root respiration; R_{CWD} , coarse woody debris respiration; R_{soil} , soil respiration; R_{stem} , above-ground woody respiration; R_{leaf} , leaf dark respiration. All units are $\text{Mg C ha}^{-1} \text{ year}^{-1}$.

interactions of particular systems, and the relatively new realms of Earth System science and global change ecology, where tropical forests have been recognized as a major influence on global biogeochemical cycles and atmospheric function. These new disciplines take the philosophical perspective of ecosystem ecology up further in scale, treating whole biomes or the global biosphere as the primary unit of study. The *modus operandi* of ecosystem ecology has been site-specific studies, often involving laborious data collection in sometimes challenging locations. In contrast, the core toolkit of the terrestrial aspects of Earth system science is increasingly centred around terrestrial ecosystem model simulation, coupled with satellite remote sensing data and eddy covariance flux tower data, but needing to be grounded with field data (and ideally networks of field sites) where possible. One of the key challenges is to work out how much detail is needed to accurately represent the function and sensitivity of tropical forests in the Earth's system. Do details in the processes of carbon production, allocation and turnover matter? Are there important biogeographical differences in

ecosystem function between, for example, the legume-rich forests of Amazonia and the dipterocarp-dominated forests of SE Asia that affect their ecosystem-level properties? Is it sufficient to treat a tropical canopy as a homogenous single tropical 'species', or better to divide it into functional groups, trait spectra, or collections of species? How much biological detail is appropriate before it becomes unwieldy and unhelpful? Through its focus on quantitative flows of carbon, water and nutrients, the currency of Earth system science, ecosystem ecology is well-placed to act as an interface between ecology-focussed field studies and Earth System science.

In this study, I review and explore what the last few decades of research have revealed about the productivity, carbon cycling and metabolism of tropical forest vegetation, drawing on primary productivity, forest inventory and eddy covariance studies. There are many other equally important aspects of tropical ecosystem ecology (e.g. decomposition, soil ecosystem processes, soil carbon turnover, remineralization and recycling of nutrients) but these are worthy of a separate review and not

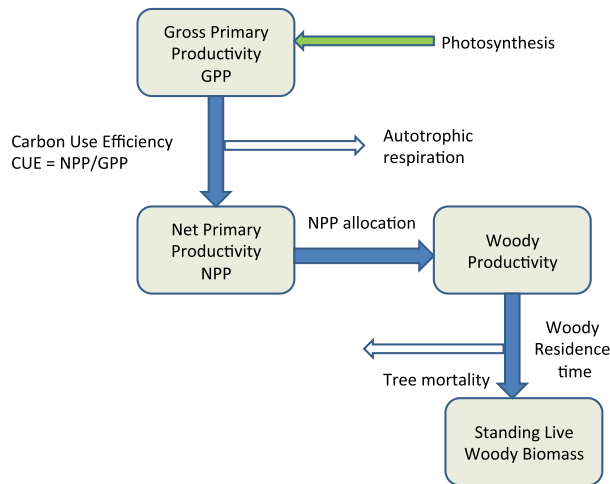


Fig. 2. A framework for understanding the carbon cycle of forests. The pathway shows the key processes linking photosynthesis and the woody biomass of a forest. Much effort in terrestrial ecosystem models has gone into accurate representation of the first process in this pathway (photosynthesis) but three other processes can be equally important: autotrophic respiration (or carbon use efficiency, CUE), allocation of net primary productivity, NPP, and mortality (or woody biomass residence time).

covered here. Part of this work is a synthesis of recent literature, and part presents new data emerging from our recent work across Amazonia. In the limited space of this article, I do not dwell on methodological issues and limitations; these are substantial but are covered elsewhere in the literature (Clark *et al.* 2001; Malhi *et al.* 2009b; Metcalfe *et al.* 2010). Rather I focus on what insights are revealed and questions opened up by the recent availability of data.

Table 1. Values of gross primary productivity (GPP), net primary productivity (NPP) and carbon use efficiency (CUE) for mature tropical forest sites where GPP has been measured, at given latitude (lat.) and longitude (long.). Units of GPP and NPP are $\text{Mg C ha}^{-1} \text{ year}^{-1}$. Elevation is in m a.s.l. Top-down GPP (GPP_{td}) is calculated from eddy covariance measurements, and bottom-up GPP (GPP_{bu}) is calculated from summing components of NPP and autotrophic respiration. Estimates of GPP and CUE from the Andes are from an unpublished study by Y. Malhi *et al.* (unpublished data)

Site	Lat.	Long.	Elevation	GPP _{td}	GPP _{bu}	NPP	CUE	Sources
<i>Mae Klong</i>	14.58	98.85	160	32.3				Hirata <i>et al.</i> (2008)
<i>Sakaerat</i>	14.48	101.92	535	38.1				Gamo <i>et al.</i> (2005)
<i>Pasoh*</i>	2.97	102.30	75–150	31.2		12.8	0.41	Takanashi <i>et al.</i> (2005b), Kosugi <i>et al.</i> (2008), Kira (1978)
<i>Palangkaraya</i>	–2.35	114.03	30	33.0				Hirano <i>et al.</i> (2007)
<i>Xishuangbanna</i>	21.93	101.27		25.9	26.0	8.8	0.34	Tan <i>et al.</i> (2010)
<i>Caxiuanã</i>			15	31.2	31.4	10.0	0.32	Malhi <i>et al.</i> 2009b
<i>Tapajós</i>			200	31.4	29.3	14.4	0.46	Malhi <i>et al.</i> 2009b
<i>Manaus</i>			90	30.4	29.9	10.1	0.33	Malhi <i>et al.</i> 2009b
<i>Caxiuanã drought control</i>	–1.72	–51.46	15	31.2	33.0	9.5	0.30	Metcalfe <i>et al.</i> 2010
<i>Caxiuanã drought</i>	–1.72	–51.46	15	27.0		7.4	0.27	Metcalfe <i>et al.</i> 2010
<i>Tono</i>			1000		24.9	7.3	0.29	Malhi <i>et al.</i> , unpublished
<i>San Pedro</i>			1500		26.9	10.8	0.40	Malhi <i>et al.</i> , unpublished
<i>Wayqecha</i>			3025		19.6	8.4	0.43	Malhi <i>et al.</i> , unpublished
<i>La Selva</i>	10.43	–80.02	80–150	29.5				Loescher <i>et al.</i> 2003
<i>Paracou</i>	5.28	–52.91	10–40	37.3				Bonal <i>et al.</i> (2008)

*The values shown for Pasoh incorporate estimates of NPP and GPP_{bu} from the 1970s, and values of GPP_{td} from the 2000s, three decades later. Given ongoing and rapid atmospheric change, the data from these two periods may not be strictly comparable.

There are many aspects of forest carbon cycling that can be considered; to limit scope, I focus on the relationship between photosynthesis, productivity and biomass, the latter two being two of the most apparent aspects of tropical forests and amongst the aspects most frequently noted by early scientist–explorers. I present a framework for this analysis in Fig. 2, which presents a causal chain linking GPP to biomass. The tropical ecological and natural history literature is replete with assumptions that productivity is somehow related to biomass, that tall, majestic forests must somehow be more productive than shorter forests. As we shall see below, this is rarely the case, as there are a number of intermediate steps linking photosynthesis to biomass. I consider each item in the chain of influence in Fig. 2 in turn.

The gross primary productivity of tropical forests

The GPP is the rate of fixation of CO_2 by photosynthesis in the forest canopy, and as such is the primary measure of carbon supply and metabolic activity in the canopy. A large amount of empirical and theoretical tropical ecosystem research has focussed on determining the GPP of tropical forests, and how it is constrained by water supply, light and nutrients. Table 1 lists a number of intact tropical forest sites where GPP has been directly estimated, either ‘top–down’ through eddy covariance studies or ‘bottom–up’ through biometric studies. The list is probably not exhaustive but represents a range of forests from the Neotropics and Asia. To date (to my knowledge), there has been no substantive study published for African tropical forests, although my research team is currently investing efforts in several sites in Central and West Africa.

At sites where there are both independent top-down and bottom-up estimates of GPP, there tends to be a fair degree of consistency in measurements, suggest that the most significant aspects of the carbon cycle are being captured by both approaches (or, less parsimoniously, that both approaches have a systematic bias). In all moist lowland forests, the GPP appears to range between 30 and 40 Mg C ha⁻¹ year⁻¹. There are hints that the higher values are found on more fertile soils, but without a consistent soils data set it is difficult to draw a definitive conclusion on this. GPP appears to be reduced at the drier or more seasonal sites, as would be expected as the length of the growing season is reduced, although the Mae Klong site in Thailand (Hirata *et al.* 2008) appears to break from this pattern. GPP also appears reduced in tropical montane systems, which may be a direct effect of lower temperatures on leaf photosynthetic parameters, an indirect effect of nutrient availability, or reduction in light availability in the cloud forest.

An insight that has been established from the eddy covariance studies is that, per unit of light, tropical forests are no more productive than temperate broadleaf forests in their peak growing season (e.g. Hirata *et al.* 2008). The high productivity of wet tropical forests appears almost entirely derived from the absence of a dormant period (winter or dry season), rather than an intrinsic high productivity associated with, for example high diversity or high temperatures. Flux studies have shown that many moist tropical forests can have some form of dry season moisture limitation (e.g. in Amazonia: (Malhi *et al.* 1998; Bonal *et al.* 2008) and can be light-limited in the wet season, but overall many moderately seasonal tropical forests exhibit fairly constant GPP over the annual cycle.

The fairly consistent results emerging from tropical eddy covariance sites enable attempts to scale to a global level. How significant are tropical forests in the global carbon cycle? Beer *et al.* (2010) used data-driven scaling approaches to scale up from the eddy covariance measurements to the globe (Fig. 3). They estimated total global terrestrial GPP to be 122 Pg C year⁻¹, of which tropical forests contribute about 41 Pg C year⁻¹, 34% of the global total. Tropical savannas and grasslands contribute a further 26%, while covering an area twice as

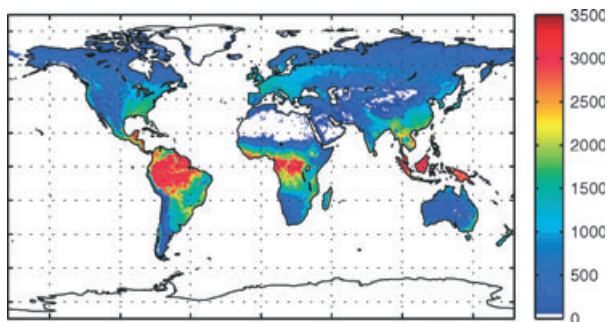


Fig. 3. The average gross primary productivity (GPP) of the land surface, over the period 1998–2005 (from Beer *et al.* 2010). The analysis is based on a world-wide network of eddy covariance flux measurements, extrapolated to the globe using five data-driven approaches that incorporate climate and remote sensing information. The figure shows the median of the five outputs. Units of GPP here are g m⁻². 100 g m⁻² = 1 Mg ha⁻¹.

large as the tropical forests. Hence, in total, tropical biomes account for about 60% of the total terrestrial land surface metabolism. In comparison, boreal and temperate forests account for 8 and 10 Pg C year⁻¹, respectively. In terms of terrestrial metabolism, we live on a predominantly tropical planet.

Carbon use efficiency

The carbon use efficiency (CUE), is defined as the ratio of NPP to GPP. NPP is the rate of production of biomass and organic compounds by the plant or ecosystem, which can be in the form of woody structures, leaf and reproductive tissues, or less obviously as root exudates, carbon transfers to mycorrhizal associations or nitrogen fixers, as volatile organic compound emissions from the canopy, or as storage as non-structural carbohydrates. The remainder of GPP is utilized for the internal metabolism autotrophic respiration of the plants within the ecosystem.

There has been debate as to the degree to which the CUE is invariant with a value of CUE *c.* 0.5 (Dewar, Medlyn & McMurtrie 1998; Waring, Landsberg & Williams 1998). The key question is to what extent is autotrophic respiration tightly coupled to GPP and hence limited by carbohydrate supply, or to what extent is it more related to biomass maintenance costs (Reich *et al.* 2006), sensitive to environmental factors such as temperature, or optimal allocation decisions within a plant.

It has been suggested that old-growth forests tend to have lower CUE than younger and secondary forest (Litton, Raich & Ryan 2007). However, the literature report a wide range of CUE values, ranging from *c.* 0.2 to *c.* 0.8 (Litton, Raich & Ryan 2007), although theoretical calculation of growth efficiency and respiratory costs associated with maintenance, nutrient acquisition and transport suggest it should be constrained between 0.2 and 0.65 (Amthor 2000). There are very few estimates for tropical forests; the estimates that we are aware of for mature systems are presented in Table 1. For the site at Pasoh, Malaysia, we have combined Kira's classic 1978 study of NPP components mentioned above with a recent value of GPP derived from eddy covariance (Hirano *et al.* 2007). This approach assumes no net change in fluxes between the 1970s and the 2000s, which may be unlikely (see below).

The few tropical sites that have reported CUE tend to produce estimates within the range 0.30–0.40, both in Amazonia and in Asia (Table 1). This also seems to apply to tropical montane forest sites, which have a cooler mean temperature. It may be that old-growth systems have higher biomass maintenance and defensive costs that raise respiration rates (De Lucia *et al.* 2007). Part of the difference may simply be related to variation in CUE with life stage. It is likely that young trees allocate more carbon to NPP as they compete spatially for light and nutrients, but older trees invest more in maintenance of their large existing biomass, and perhaps also give greater priority to maintenance of chemical defence of existing biomass relative to acquisition of new biomass. The demography of forest stands recovering from disturbance, or in the more productive and high turnover steady state found on more fertile sites, would tend towards younger, faster growing trees and hence towards higher CUE. Another possibility that has been

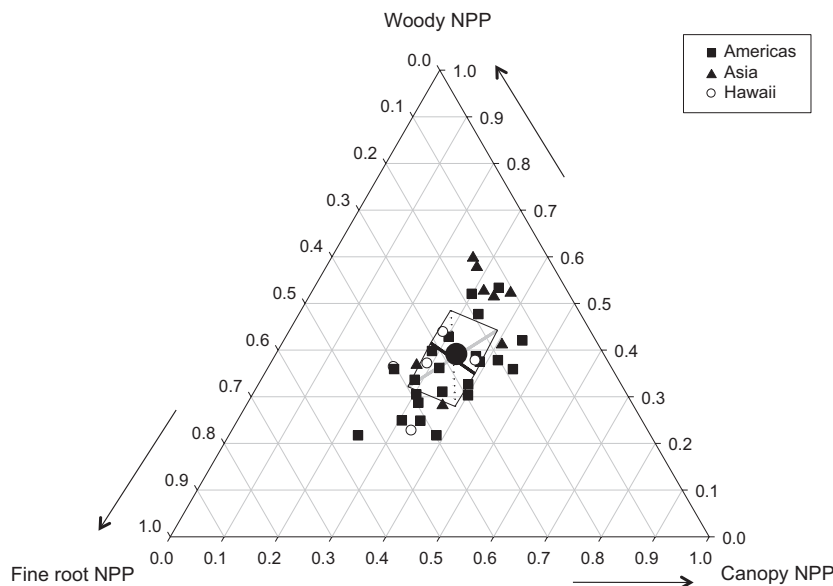


Fig. 4. Ternary diagram for allocation of net primary productivity (NPP) in tropical forests: woody NPP (includes branch and coarse root NPP), leaf litter NPP (includes reproductive NPP) and fine root NPP for 35 individual field sites and average amongst all sites (solid circle) surrounded by standard deviation (grey line is standard deviation for fine root NPP, black line is standard deviation for canopy NPP, dotted line is standard deviation for woody NPP). The symbols indicates geographic region. Modified from Malhi, Doughty & Galbraith (2011).

raised is that tropical ecosystems have excess carbon supply due to plentiful light in the upper canopy and insufficient nutrient availability, and release much of this excess carbon in 'idling respiration', waiting to reallocate it if a rapid increase in NPP is needed in the wake of a disturbance (Chambers *et al.* 2004). The former hypothesis suggests that differences in tree demography explain differences in CUE, and the latter suggests individual trees can alter their CUE in response to disturbance. It should be possible to explicitly test these alternative hypotheses with future field studies.

Net primary productivity and its allocation

The next step of the carbon pathway is the allocation of NPP between its components, the major ones of which are canopy NPP (leaves, flowers and fruit), woody production (stems, branches, twigs and coarse roots) and rhizosphere (fine root and exudate production or transfer of carbon to symbionts). There are methodological issues with measurements of all these components, ranging from herbivory and *in situ* decomposition of canopy litterfall, the challenge of measuring root exudates, and woody biomass allometric equations. Malhi, Doughty & Galbraith (2011) recently conducted a review of NPP allocation in tropical forests globally, synthesizing results from 35 tropical forest sites where canopy, wood and fine root NPP are reported, and 71 sites where canopy and woody NPP are reported. They found that, on average, the allocation of NPP between its three main components is relatively invariant and fairly close to equal partitioning (mean $34 \pm 6\%$ for canopy, $39 \pm 10\%$ for wood, $27 \pm 11\%$ for fine roots), but there is substantial site-to-site variation (Fig. 4). Across sites, the major component of variation appears to be shifting allocation between wood and fine roots, with allocation to the canopy

being a relatively invariant component of total NPP. This existence of a 'wood – fine-root' trade-off has recently been posited by (Dybzinski *et al.* 2011) in a theoretical framework for old-growth stands. Their framework predicts the most competitive allocation of NPP in invading trees as they compete with established trees in old-growth stands where the stand is dual-limited by light and nutrients. Self-shading ultimately limits returns on foliage investment, whereas competitive considerations dominate investment in fine roots vs. wood.

This trade-off gives a theoretical underpinning as to why litterfall is a better indicator of total NPP than stem growth or fine root productivity, as the fractional allocation to canopy NPP is relatively invariant. A side-benefit of this is that litterfall measurements can provide a reasonable estimate of total NPP, a relationship that was first posited by (Bray & Gorham 1964). Chave *et al.* (2010) compiled data on litterfall for 81 sites in South American tropical forests and found a mean litterfall rate of $4.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (SD $0.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). Using the suggested multiplying factor of 2.42 (Malhi, Doughty & Galbraith 2011), this suggests mean South American tropical NPP values of around $10.6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$.

It is worth noting that wood allocation (including coarse roots and branch turnover) is typically only 39% of NPP, and above-ground stem-based production (excluding branch turnover), the usual benchmark of productivity for foresters and forest ecologists, is typically only 25% of NPP (Malhi, Doughty & Galbraith 2011). Moreover, with typical values of CUE of *c.* 0.3, stem-based production accounts only about 10% of the GPP. Tree growth is simply a visible and fairly long-lived, but relatively minor, component of the much larger internal carbon cycle of tropical forests. Small variations in CUE and NPP allocation can thus have a profound impact on tree growth.

The residence time of NPP

The components of Fig. 2 thus far considered enable us to understand how wood productivity (i.e. the observed mean growth rate of trees in a forest) is a function of controls on GPP, on CUE and on the allocation of NPP between canopy, rhizosphere and woody tissue. To understand how all this relates to the biomass and structure of a forest, we need to finally consider the mean residence time of woody tissue in living trees, τ_w , which is strongly related to, but not identical to, the mean lifetime of trees. Calculation of the mean lifetime of trees in a forest are influenced by the predominance of small trees, whereas mean woody biomass residence time is much more influenced by the lifetimes of medium and large trees.

For a near-equilibrium ecosystem such as an old-growth tropical forest, τ_w can be estimated by dividing the above-ground woody biomass by the above-ground woody productivity. Such an approach to calculating τ_w does not work for non-equilibrium systems such as secondary forests, where the observed biomass is below equilibrium values and hence does not reflect background mortality rates.

Assumption of a fairly constant τ_w is implicit in classic descriptions of high biomass forests that assume high biomass is somehow an indicator of high productivity, and many current terrestrial ecosystem models assign a fixed value to τ_w . Yet the last decade of field data has shown a surprising result. Using data from the RAINFOR field network of long-term plots in primary forests across Amazonia, Malhi *et al.* (2006) demonstrated that τ_w is a strong inverse function of woody productivity. Forests that had high productivity had short residence times and vice versa. Put another way, woody biomass showed almost no relationship to woody productivity (in fact, there was a slight negative relationship) – the higher the rate of woody biomass creation in an old-growth forest, the higher the rate of biomass loss through mortality.

Why would this be the case? One possibility is a system-level constraint on biomass. The biomass of a forest may be constrained by canopy height (itself a function of mechanical constraints – (King *et al.* 2009) – and possibly hydrological constraints) and by crown space availability (a function of mechanical constraints on mean crown size), both constraints ultimately reflecting competition for light resources. Increasing wood productivity (a ‘bottom-up’ input) in this system simply intensifies competition for light resources, leading to higher rates of mortality and turnover. In a global review, Stephenson *et al.* (in press) recently addressed the question of the correlation between productivity and mortality, and presented several hypotheses that might help to explain the correlation. These include the effect of competition, which intensifies with increasing resource availability, the increased occurrence of plant enemies in more productive areas, trade-offs between growth and defence, trade-offs between growth and hydraulic safety and trade-offs between reproduction and persistence. The life-history trade-off between fast growing, short-lived species that have a competitive advantage for light at the expense of defences against mechanical breakage and herbivore or pathogen attack, and slow-growing long-lived species that invest

more in defending their resources, has long been noted in the context of tropical forests. High productivity sites with higher nutrient availability may favour the rapid growth strategy over the defence strategy.

The insight that residence time is variable has important implications for understanding and predicting biomass in primary forests. For example, western Amazonian forests have, typically, twice the wood productivity of eastern Amazonian forests (Malhi *et al.* 2004) yet have similar or lower biomass (Malhi *et al.* 2006). The high productivity in the west is strongly correlated with the higher soil fertility and in particular phosphorus status (Aragao *et al.* 2009; Quesada *et al.* 2009) on the younger soils. If the variation in residence time is not incorporated into terrestrial model simulations, the biomass of western Amazonian forests can be greatly overestimated (Delbart *et al.* 2010).

Variation in tree growth and mortality rates has a profound effect on the physical and trophic structure of forests, through changes in light environment, necromass availability, herbivore and pathogen pressure, and nutrient supply and recycling rates. It is quite conceivable that τ_w is the single most important parameter that describes why one tropical forest is different from another.

Summary and reflections

This synthesis pulls together some insights into the carbon cycle of tropical forests that have been gleaned from the last few decades of research, in particular with the spread of the quantitative, whole-system approach to ecosystem ecology pioneered by Odum, Kira and others, and with the spread of canopy-atmosphere flux monitoring. The focus of the whole-system approach has been on rigorous quantification of flows of carbon, energy and nutrients within the system (here we have focussed on carbon) and in doing this, we can see that new insights have emerged on some age-old questions.

Why are tropical forests so productive? We have learned that the relative productivity of tropical forests over temperate or drier systems can be largely explained by the lack of a dormant period in the winter or dry season. However, temperature probably has some effect (direct or indirect) on rates of GPP, as new data from tropical montane and submontane systems suggest. Within the wet tropical zone, variations in light and climate seem to have relatively little effect on GPP. Field studies have shown the strongest correlations of wood productivity or NPP with soil phosphorus availability and leaf phosphorus concentrations (Aragao *et al.* 2009; Quesada *et al.* 2009), supporting the suggestion that many tropical systems are likely to be P limited (Porder *et al.* 2007; Vitousek *et al.* 2010). Our understanding of this is far from complete however, and in particular of the role that key micronutrients such as calcium, sodium and potassium may play.

We have learned that the most visible aspect of forest productivity, the woody productivity or rate of tree growth, accounts for only about 10% of GPP, and small shifts in CUE or NPP allocation can have a disproportionate effect on tree growth rates. Much attention has focussed on understanding

and modelling the magnitude and constraints on GPP, yet understanding NPP allocation and in particular CUE is equally as important, and needs much greater attention. It seems that CUE tends to be lower in many primary tropical forests than in other systems, suggesting that the productivity benefit of higher GPP is offset to some extent by the loss of higher autotrophic respiration. Why this would be the case is not yet clear.

Finally, it is apparent that old-growth, mixed-age systems have particular emergent properties that are not well understood and are not obvious from the properties of individuals within that system. One example is the posited trade-off between wood and fine roots, with relatively invariant allocation to the canopy, which may result from competition in light-limited environments. Another is the strong dependence of residence time and tree mortality on wood productivity, which results in biomass being almost independent of productivity. Such emergent properties are useful when we try to generalize from individuals to ecosystems, but also present a major challenge for those attempting to model and understand the future of tropical forests. If rising atmospheric CO₂ concentrations stimulate wood productivity, will this mean that in the long-term there will be almost no net increase in biomass in intact tropical forests, but rather just an acceleration of tree turnover? The increase in biomass in old-growth Amazonian and African forests currently being observed (Phillips *et al.* 1998; Baker *et al.* 2004; Lewis *et al.* 2009) may be a transient effect caused by the demographic lag between recruitment and mortality, and the concurrent increase in turnover (Phillips *et al.* 2004) may be of much greater long-term consequence, both for the ecology and community composition of tropical forests as they shift towards a more gap-dominated state, and for the rate of CO₂ build-up in the atmosphere as the tropical biomass carbon sink dwindles. Almost all of the current generation of terrestrial ecosystem models are not equipped to incorporate such structural feedbacks, and correct understanding and representation of these interactions is a subject where tropical forest ecology has a major contribution to make.

Looking forward: tropical ecosystem ecology of the Anthropocene

The current rate of human-induced change of Earth system properties is so great that it has been argued that the Earth has entered a new geological era, the Anthropocene (Steffen *et al.* 2011), posited to have begun in the 1700s or even earlier but really apparent in its influences only since the 'Great Acceleration' of the mid-20th century (Steffen *et al.* 2011). Examples of Anthropocene influences include changes in atmospheric and ocean properties and biogeochemistry, biome cover change or faunal extinction, or the 'new Pangaea' (Rosenzweig 2001) being created by increasing mixing of species previously separated by biogeographical boundaries. The term Anthropocene is attracting widespread usage, although it has not yet been formally adopted.

In the field of ecology, the consequence of an Anthropocene-centred world view is a recognition that probably all eco-

systems are currently in a state of disequilibrium, not only because of direct human pressures but also because of changes in the atmosphere and oceans. In the tropical forest regions, the main characteristics of the current phase of the Anthropocene are the ongoing conversion of the tropical forest landscape into a secondary forest or fragmented landscape (Wright & Muller-Landau 2006), coupled with faunal shifts such as the decline of medium and large animals because of overhunting and habitat restriction (although the most important large-animal extinctions in many areas may well have occurred with human-induced megafaunal extinctions in the Pleistocene and Holocene: Barnosky 2008). Coupled with these direct pressures, there are indirect pressures from rising atmospheric CO₂ and greenhouse gas concentrations, resulting in warming atmospheric conditions. Surface air temperatures in tropical rain forest regions have been rising at about 0.25 °C decade⁻¹ over the last three decades (Malhi & Wright 2004) and are expected to increase by 3–6 °C this century (Zelazowski *et al.* 2011). Climate change is also expected to increase seasonality and variability of tropical rainfall, resulting in probable but poorly predicted changes in spatial rainfall patterns (Malhi *et al.* 2009a; Zelazowski *et al.* 2011). There is evidence that even remote tropical forests are already changing in response to the atmospheric changes with shifts in dynamics (Phillips *et al.* 2004), biomass (Baker *et al.* 2004; Lewis *et al.* 2009) and composition (Phillips *et al.* 2002; Feeley *et al.* 2011a), and species ranges may be beginning to migrate upslope in response to rising temperatures (Chen *et al.* 2009; Feeley *et al.* 2011b).

At the level of ecosystem ecophysiology, a key question is: are there metabolic thresholds where tropical forest functioning begins to decline with rising temperatures? In the long-term, probably not within the 3–6 °C warming expected over this century. There is evidence that tropical forests were abundant in the Palaeocene–Eocene Thermal Maximum, 55 million years ago (Jaramillo *et al.* 2010), when temperatures were about 5 °C higher than present, and in the Miocene Climate Optimum (Hoorn *et al.* 2010). Indeed, tropical forests may increase in productivity through a combination of higher CO₂ and temperature increasing the rates of mineral cycling. There are, however, likely to be variable responses across species, resulting in reorganization of the species composition of the ecosystem, which in turn may affect ecosystem properties. A key factor affecting community composition is the rapid rate of warming expected this century. For example, it has been suggested that Amazonia warmed at a rate of *c.* 0.1 °C century⁻¹ at the end of the last glacial (Bush, Silman & Urrego 2004), and on average around 0.05 °C century⁻¹ at the Palaeocene–Eocene Thermal Maximum (Jaramillo *et al.* 2010). The warming rates of around 4 °C century⁻¹ projected for this century are 1–2 orders of magnitude greater. The 21st century rate of warming corresponds to a horizontal 'velocity of climate change' of about 1–10 km decade⁻¹ in the lowland wet tropics (Loarie *et al.* 2009), a velocity that challenges species dispersion and migration rates, and hence will affect community composition.

If any tropical forest regions dry substantially, this would lead to a shift to drier and lower biomass forest biomes, and

the possible loss of forested areas. Regions that appear vulnerable to drying include Central America, Eastern and Southern Amazonia, West Africa and Peninsular Southeast Asia (Zelazowski *et al.* 2011). The climate risk to the Amazon forest may have been overstated based on a few high-profile studies (Malhi *et al.* 2009a), but recent occurrence of droughts and associated tree mortality does suggest the potential of major drought-induced changes in Amazonia (Phillips *et al.* 2009). Africa may be the major tropical forest region most sensitive to climate change. There have been rapid changes in tropical forest composition and cover in this area in the past (e.g. even in the mid-late Holocene: Maley 2002; Ngomanda *et al.* 2007) and it is likely that the lower plant diversity in African forests is a direct result of the bottlenecks of rapid change through which the forests have passed (Maley 2002; Parmentier *et al.* 2007). Conversely, much of the extant tropical African tree assemblage may have passed through climate-driven extinction filters, and the surviving species may be more adaptable to rapid climate change, and particularly changes in rainfall regime.

How the forest primary productivity interacts with nutrient cycles is a major source of uncertainty in projecting the future ecosystem ecology of the tropics. If results from temperate forest Free Air Carbon Dioxide Enrichment experiments (all in temperate secondary forests or plantations) are extrapolated to the tropics, allowing for higher photorespiratory effects at warmer temperatures (Hickler *et al.* 2008), we would expect a typical lowland tropical forest GPP to have risen by 18% from pre-industrial values. This suggests the current observed GPP values in Table 1 are already substantially increased above background Holocene rates. Furthermore, GPP values would be projected to increase from the current *c.* 30 Mg C ha⁻¹ year⁻¹ to *c.* 36 Mg C ha⁻¹ year⁻¹ in the 500 ppm CO₂ world that we are on track to reach by 2050, and perhaps 48 Mg C ha⁻¹ year⁻¹ in the projected 800 ppm by 2100 (all concentrations are mean of multiple GCMs under the IPCC SRES A2 emissions scenarios). We do not know whether ecosystem GPP can in reality attain and maintain such high values over the long term, but these estimates do suggest that the tropical forests that we are observing and studying today may already be far from physiological steady state.

Will nutrient supply constrain this large increase in productivity, or will more rapid decomposition and recycling, tighter recycling and more active root foraging enable such an increase? What consequences would there be for the structure and composition of the floral and faunal communities? In areas that become dry, how rapid a shift in forest structure can we expect, or is there inbuilt inertia in the system (Malhi *et al.* 2009a)? Ongoing studies and monitoring of tropical ecosystem functioning and composition are essential to obtain answers to these questions, and our default expectation should be one of change rather than one of equilibrium. Indeed, if the systems are not shifting in functioning and composition as a result of these external pressures and the large potential for change, we need to understand why. As shifts in tropical forest communities become apparent, we also need to move from a metabolic understanding of whole stands to an understanding of compo-

nents of the metabolism of component species, or at least functional groups, to better understand the interaction between community composition and ecosystem-level processes.

Answering these questions matters not only to those concerned about the future of the tropical biome, but also to those concerned about the future of the Earth's System, because the response of tropical biomes has a substantial influence on the rate of climate change world-wide. Intact tropical forests currently appear to be increasing in biomass and absorbing carbon from the atmosphere at a rate of 1.1 ± 0.3 Pg C year⁻¹, slowing down the rate of global warming by about 15% (Malhi 2010). If there are shifts in the metabolism and carbon cycling of tropical forests, this carbon sink could turn into a source and an accelerator of climate change. Hence, it is important to establish baseline measurements of the current carbon cycle of forests and continue to revisit these sites over the 21st century to provide insights into ongoing changes and an early warning system of potential severe changes. As in almost all areas of ecology, the ecosystem ecology of tropical forests is turning from the study of systems assumed to be in steady state to the study of systems in transition.

In many areas, the realm of the wet tropical forest has already changed far beyond that described by the early scientist-explorers, from the monotonous oil palm expanses of much of Sumatra and Borneo, the silent, overhunted forest fragments of West Africa, to the horizon-spanning cattle ranches and soy fields of Mato Grosso ('the great wood'). It is perhaps stating the obvious that studying the remaining forests in these areas is the study of forests in transition. Yet there is still much of the tropical biome left, with fair prospects of persisting throughout the century, whether in the form of fairly untouched primary forest or spreading secondary forest. How will these biomes, these Anthropocene refugia, fare in the substantially altered atmosphere of the 21st century, and what role do they have yet to play in the functioning of the Earth System?

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