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The Structure, Distribution, and Biomass of the World's Forests

Yude Pan,[1] Richard A. Birdsey,[1] Oliver L. Phillips,[2] and Robert B. Jackson[3]

[1]US Department of Agriculture Forest Service, Newtown Square, Pennsylvania 19073; email: ypan@fs.fed.us, rbirdsey@fs.fed.us

[2]School of Geography, Leeds University, Leeds LS2 9JT, United Kingdom; email: O.Phillips@leeds.ac.uk

[3]Nicholas School of the Environment, Duke University, Durham, North Carolina 27708; email: jackson@duke.edu

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Keywords

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Abstract

Forests are the dominant terrestrial ecosystem on Earth. We review the environmental factors controlling their structure and global distribution and evaluate their current and future trajectory. Adaptations of trees to climate and resource gradients, coupled with disturbances and forest dynamics, create complex geographical patterns in forest assemblages and structures. These patterns are increasingly discernible through new satellite and airborne observation systems, improved forest inventories, and global ecosystem models. Forest biomass is a complex property affected by forest distribution, structure, and ecological processes. Since at least 1990, biomass density has consistently increased in global established forests, despite increasing mortality in some regions, suggesting that a global driver such as elevated CO_2 may be enhancing biomass gains. Global forests have also apparently become more dynamic. Advanced information about the structure, distribution, and biomass of the world's forests provides critical ecological insights and opportunities for sustainable forest management and enhancing forest conservation and ecosystem services.

1. INTRODUCTION

Gross primary production (GPP): carbon assimilation from photosynthesis by vegetation per unit area and time

Forests cover 4.03 billion hectares globally, approximately 30% of Earth's total land area (FAO 2010). They account for 75% of terrestrial gross primary production (GPP) (Beer et al. 2010) and 80% of Earth's total plant biomass (Kindermann et al. 2008) and contain more carbon in biomass and soils than is stored in the atmosphere (Pan et al. 2011a). Forests also harbor the majority of species on Earth and provide valuable ecosystem goods and services to humanity, including food, fiber, timber, medicine, clean water, aesthetic and spiritual values, and climate moderation (Jackson et al. 2005, McKinley et al. 2011). Moreover, more than 200 million of the world's poor rely directly on forests for energy, shelter, and their livelihoods (SCBD 2010).

Forests are distributed across the globe (see the sidebar, What Is a Forest?). Thirty-one percent of Earth's total forest area is found in Asia (including Asian Russia), followed by 21% in South America, 17% in Africa, 17% in North and Central America, 9% in Europe, and 5% in Oceania (FAO 2010). Globally, 5% of forests are plantations generally used for commercial purposes.

Knowledge of the structure, distribution, and biomass of the world's forests is advancing rapidly because of improved global observation systems and analysis techniques (Asner et al. 2012, Saatchi et al. 2011). New satellite and airborne observation systems, improved land-based inventory systems, and ecosystem models are providing forest maps with unprecedented resolution (Running et al. 2009, Shugart et al. 2010). Three-dimensional remote sensing allows researchers to estimate forest canopy height, map the world's forests, and estimate forest biomass and carbon stocks (Lefsky 2010, Saatchi et al. 2011). New, standardized, continent-spanning field networks (e.g., Malhi et al. 2002, Smith et al. 2009) are addressing many ecological issues, from forest succession to vegetation-atmosphere interactions. New tools are also providing decision support for forest management, conservation biology, and ecological restoration.

In this review we address the structure, distribution, and biomass of the world's forests with the following underlying question: What do we know today through new technologies and approaches that we did not know a decade or two ago? We begin by identifying the processes and factors that define the occurrence, formation, and physiognomy of the world's forests. We describe how climate strongly determines forest distribution and structure, acknowledging that disturbances and succession add important landscape complexity. We further examine the connections between productivity, mortality, and biomass and illustrate how these factors, including human disturbances, determine large-scale patterns of forest biomass. Woven into each section is information about new

WHAT IS A FOREST?

As defined by the Global Forest Resource Assessment, a forest is land spanning more than 0.5 ha with trees taller than 5 m and with a canopy cover of more than 10% [or trees able to reach these thresholds in situ (FAO 2006)]. This definition does not include land that is predominantly agricultural or urban, even if such land has some tree cover. Forest lands that are temporarily treeless because of harvest or disturbance are included. Because of these land-use considerations, it is critical not to confuse the FAO definition of a forest with "forest cover," which is based only on the presence or absence of trees and is the product of most remote sensing–based estimates and maps. The implications of failing to account for these differences can be profound. For example, Hansen et al. (2010) used *MODIS* and *Landsat* imagery to document a 6% loss of forest cover (120,000 km^2) in the United States from 2000 to 2005. In contrast, the forest inventory based on ground plots using the FAO definition indicated a net gain of forest land during the same period (Smith et al. 2009). The difference is largely due to timber harvesting, which temporarily removes forest cover but does not usually change land use.

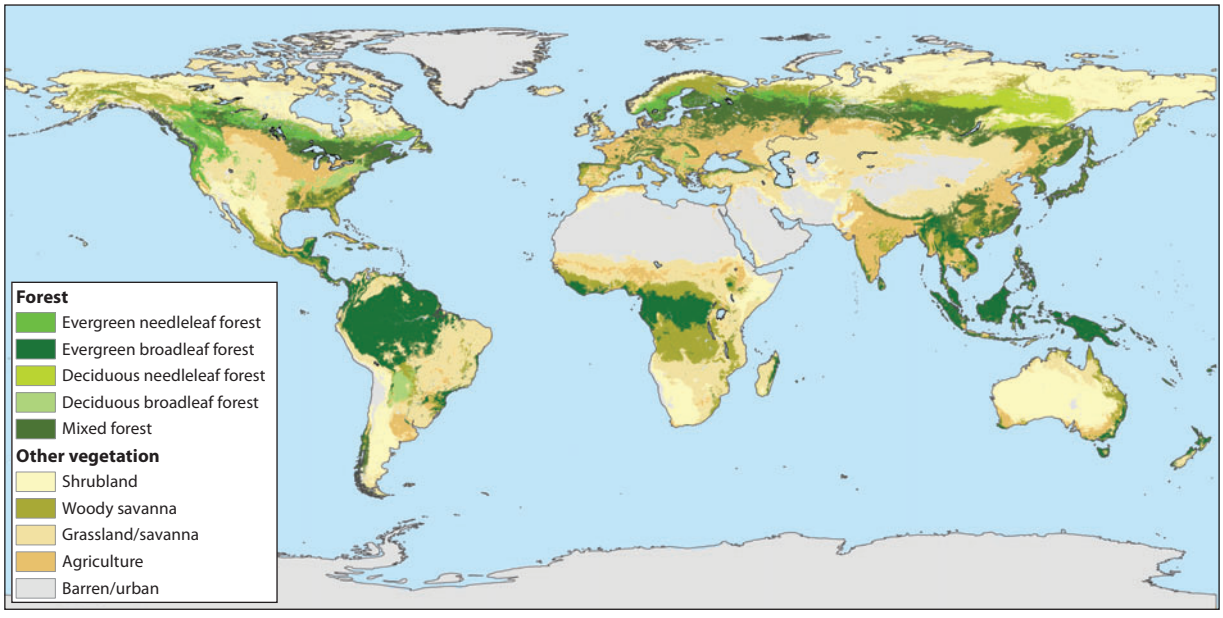

Figure 1

2011 global forest cover map, based on *MODIS* satellite data at 500-m resolution and on IGBP-DIS (The International Geosphere-Biosphere Programme Data and Information System) land-cover classifications (**http://www.landcover.org**).

technologies used to observe forest structure and distribution, as well as opportunities to sustain or improve forest conditions and services. Our goal is to shed light on the world's forests and how they have been shaped through time, facilitating greater appreciation of their irreplaceable services to humanity.

2. WHAT PROCESSES AND FACTORS DEFINE THE LIMITS OF FORESTS?

2.1. Geography, Climate, Topography, Soil, and Environmental Variation

Distinct latitudinal bands of forest vegetation are clearly visible through satellite-based remote sensing (**Figure 1**). The latitudinal gradient corresponds primarily to the geographical distribution of climate (Woodward 1987); forests are more widely distributed in the Northern Hemisphere, where larger land masses occur. The length of the growing season decreases from the full year in the wet tropics to only 7 to 10 weeks in the boreal region. Forests with different life forms and growth forms, such as deciduous, evergreen, needle-leaved, and broad-leaved trees, are adapted to the seasonality of temperature and rainfall in their geographic region (Whittaker 1975, Woodward et al. 2004).

At a regional or local scale, topography, soil type, and other local environmental factors modify the effect of climate and shape local microclimates (Littell et al. 2008). Physiographic and topographic variabilities of mountains particularly influence regional and local climates by changing the patterns of temperature, wind circulation, and precipitation. In some situations, soils mediate water availability. High nutrient availability of soils is often associated preferentially with forests

and may partially decouple the connection between climate and tree distribution (Murphy & Bowman 2012).

Because of the correlation between the geographical patterns of forests and climate, a few major climate variables such as temperature and precipitation have been used to explain global forest distributions (e.g., Holdridge 1967, Whittaker 1975). For cold-sensitive trees, typically those growing in the tropics, minimum temperatures of ~10°C may cause mortality; in contrast, some northern deciduous broadleaf forests can survive extreme cold below −40°C when dormant tissues such as buds are protected by supercooling (Sakai 1982, Woodward 1987).

Precipitation has a more direct, mechanistic relationship to forest distribution than does temperature (Woodward et al. 2004). Along forest-to-desert gradients, trees give way to shrubs or grasses when water availability cannot meet the transpirational needs of trees (Calder 1998). Drought has particularly lethal effects, causing dieback or death of established trees and preventing seedling establishment (Van der Molen et al. 2011). In general, a minimum annual precipitation of 600 mm sets the forest distribution limit in all areas except in colder regions (400 mm), where evaporation is also low (Woodward 1987).

2.2. Disturbances, Forest Vulnerability, and Landscape-Scale Diversity

Various natural or human-induced disturbances exert profound impacts on global forests. According to a recent global assessment, more than 60% of the world's 4 billion ha of forest are recovering from a past disturbance, and 3% of the world's forests are disturbed annually by logging, fire, pests, or weather (FAO 2006). Although some nations have recently experienced an increase in forest area due to recovery from historical land uses or reforestation programs (Kauppi et al. 2006), the global forest area still decreased by between 4.1 and 6.4 million ha $year^{-1}$ over the past two decades (FAO 2012). Agricultural expansion has been the most important proximate cause of recent forest loss, accounting for 80% of deforestation worldwide, primarily during the 1980s and 1990s through conversion of tropical forests (Gibbs et al. 2007, Houghton 2007).

Climate change, induced by anthropogenic greenhouse gas emissions (IPCC 2007), is becoming another important factor that shapes forests globally (Walther 2010). Observations have documented the upward movements of tree species and tree lines in response to increased temperatures over the past few decades (e.g., Beckage et al. 2008, Kullman & Öberg 2009), and dendroecological studies show general evidence of enhanced tree recruitment and growth at the northern tree lines (Andreu-Hayles et al. 2011, MacDonald et al. 2008). Paleoecological data suggest that climate-induced migration of tree species creates new geographic distributions of forest communities and new combinations of species because the rates and direction of responses differ among species (Webb 1992). Climate change also triggers changes in disturbance regimes, such as increasing frequency and intensity of wildfires, windstorms, or insect outbreaks (Dale et al. 2001). Altered rainfall patterns and increasing temperature have caused drought and heat stress around the world and resulted in significant regional increases in tree mortality or forest die-offs, as well as regional decreases in forest productivity, often attributable to interactions with insect outbreaks and fires (Allen et al. 2010, Kurz et al. 2008, Phillips et al. 2009). Disturbances varying in type, scale, intensity, and frequency create complex mosaics of forest distribution and high landscape-scale diversity.

2.3. Classification Schemes and Mapping of Forest Distributions

Classification is a useful means for understanding spatial patterns of vegetation across natural landscapes. Correlative approaches have traditionally been used to reveal climatic controls over

vegetation distribution and to define global patterns of major biomes (e.g., Holdridge 1967, Whittaker 1975). Holdridge's life-zone system is one of the most widely used and quantitative schemes. It provides a detailed classification of global biomes based on three bioclimatic variables: long-term average annual precipitation, mean annual biotemperature, and potential evapotranspiration ratio. Whittaker (1975) simplified Holdridge's scheme and developed a biome-type classification that used only two major climate variables, temperature and precipitation, to represent the aggregate effects of gradients associated with community structure and environment. Such a classification based on both physiognomy and climate is known as a climate envelope and has been applied as the principal concept in developing global biogeography models and dynamic global vegetation models (DGVMs) for predicting global vegetation distribution (e.g., Sitch et al. 2008). However, this method has also been criticized for being "static" and somewhat subjective in that it overlooks critical biological processes and some physiological aspects of climatic impacts on plants (Stephenson 1998, Woodward et al. 2004).

Global and regional mapping of forest distribution increasingly relies on satellite remote sensing because of advantages of consistency and automated image processing. Facilitated by remotely sensed land-cover data (e.g., *SPOT* and AVHRR) and geographic information system (GIS) technology for harmonizing regional map products, various global classifications and maps have been developed (e.g., FAO 2001, Olson et al. 2001; the GLC2000). For example, the FAO (2001) defined vegetation domains by using the Köppen-Trewartha climatic system (Trewartha 1968), which has good correspondence with natural vegetation types and soils. The ecological zones were further defined by similar physiognomy, relatively homogeneous natural vegetation formations, and other ecosystem components, resulting in 13 global forest zones (**Supplemental Figure 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). Alternatively, the World Wide Fund for Nature (WWF) classification system has a more detailed level of biogeographic resolution, with 8 forest types and 867 ecoregions representing distinct biotas and habitats (Olson et al. 2001).

Although broad-scale, geographical forest zones and other global classification systems depict potential areas of forest distribution under present climatic and edaphic conditions, a remotely sensed forest-cover map provides a more objective representation of existing forest distribution (Hansen et al. 2003). Frequent observations by remote sensing are particularly well suited to revealing temporal changes in forest canopies, as well as changes in forest areas and boundaries affected by wildfires, deforestation, or afforestation (Aragão & Shimabukuro 2010, Running et al. 2009). However, at the global scale, MODIS-based observations (**Figure 1**) can currently identify only four physiognomic classes of trees (evergreen needle-leaved, evergreen broad-leaved, deciduous needle-leaved, and deciduous broad-leaved trees) and seven relatively coarse woody biome types based on trees and shrubs. Even so, remote-sensing observations reveal that the mixed classes extend across broad zones in the Northern Hemisphere (**Figure 1**) and that the distributions of biomes are often interspersed rather than sharply delineated (Woodward et al. 2004). Deciduous forests, although widespread, are intermingled with agriculture, shrubs, and grasses and rarely dominate any area. Discrepancies between potential and actual forested areas probably reflect the extent to which anthropogenic disturbances have altered climate-controlled forest biomes, particularly in temperate forest zones (**Table 1**). Because the newest remote-sensing technologies, such as hyperspectral sensors, have already been successfully applied to tree species–level classification at relatively fine scales (Clark et al. 2005), future studies may combine the capacities of *MODIS* (at 250–500-m resolution) with other high-resolution remote sensing to achieve more sophisticated global forest-cover classifications (see the sidebar, Fine-Scaled Forest Classification and Mapping). These hybrid approaches shall retain the advantage of remote sensing for timely observation of vegetation dynamics.

Dynamic global vegetation models (DGVMs): computer simulations of large-scale vegetation and its interactions with biogeochemical and hydrological cycles as a response to climate

***Satellites pour l'observation de la terre* (*SPOT*):** satellites that supply high-resolution, wide-area optical imagery of the land

Advanced Very High Resolution Radiometer (AVHRR): a radiation-detection imager used for remotely determining cloud cover and images of the planet's land surface

Global Land Cover 2000 (GLC2000): the map product from the project of the Global Vegetation Monitoring Unit of the European Commission

Moderate-resolution imaging spectroradiometer (MODIS): an instrument aboard weather satellites that acquires images of Earth in 36 spectral bands every 1 or 2 days

Supplemental Material

Table 1 Distribution and structure of the world's forests (and other woodlands)[a,b,c]

Domain	Forest biomes	Annual mean temperature (°C)	Total annual precipitation (mm)	Seasonality	Canopy height (m)	Total biomass carbon density (Mg C ha^{-1})	FAO ecological zone (M ha)	Existing forest (M ha)
Tropical 23.5°N–23.5°S All months without frost	Tropical rainforest	~20–25°C	>1,500	No dry season	25–50	145 ± 53	1,458	1,354
	Tropical moist deciduous (monsoon)	>15°C	1,000–2,000	3–5 dry months in winter	15–30	73 ± 47	1,105	795
	Tropical dry forest	>15°C	500–1,500	5–8 dry months in winter	5–20	53 ± 35	747	645
	Tropical shrublands	>15°C	200–500	8–11 dry months	3–15	71 ± 45	831	701
	Tropical mountain systems	<18°C	700–2,000	0–11 dry months	3–35	124 ± 54	453	351
	Mangrove	>18°C	700–2,000+	Highly variable	3–30	218 ± 173	–	14
	Peat swamp	>18°C	1,500–2,000+	<5 dry months	12–50	206 ± 100	–	44
Subtropical 25°N–40°N, 25°S–40°S 8+ months over 10°C	Humid forest	14–22°C	600–1,000+	No dry season	10–35	66 ± 46	468	375
	Dry forest (Mediterranean)	>7°C	300–1,000	Winter rains, dry summer	6–30	67 ± 60	159	199
	Subtropical mountain system	<12°C	500–2,000	0–8 dry months	10–30+	77 ± 41	486	408
Temperate ~40°N–54°N, 40°S–54°S 4–8 months over 10°C	Oceanic forest	5–11°C Coldest month >0°C	600–3,500+	All year growing season	50–100+	208 ± 131	181	127
	Continental	~10°C Coldest month <0°C	750–1,500+	120–250 days growing season	25–40	61 ± 31	695	473
	Mountain systems	<10°C	1,000–2,500	Variable	10–75+	59 ± 22	723	497

(*Continued*)

Table 1 (*Continued*)

Domain	Forest biomes	Annual mean temperature (°C)	Total annual precipitation (mm)	Seasonality	Canopy height (m)	Total biomass carbon density (Mg C ha^{-1})	FAO ecological zone (M ha)	Existing forest (M ha)
Boreal 50°N–55°N to 65°N–70°N Up to 3 months over 10°C	Coniferous	−12–6°C 3 months >10°C	<500	<100 days growing season	<15	48 ± 24	865	697
	Tundra woodland	−15–0°C Summer 6–14°C	150–250	35–65 days growing season	<15	7 ± 6	395	496
	Boreal mountain system	−14–5°C Summer 6–16°C	400+	50–80 days growing season	<15	19 ± 14	630	582

[a]The classification scheme is based on FAO global ecological zones (FAO 2001). Total biomass densities were derived from Saatchi et al. 2011, Pan et al. 2011a, Donato et al. 2011, IPCC 2006, and Thompson et al. 2012. Total biomass includes above- and belowground live biomass.
[b]Some systems are described by information about the ranges of mean temperatures, and some by only the mean minimum or maximum temperatures.
[c]The existing forest (and woodland) areas are based on the *MODIS* forest/woodland cover and were estimated by matching forest/woodland classes in the *MODIS* cover map with FAO ecological zones.

FINE-SCALED FOREST CLASSIFICATION AND MAPPING

In addition to global-scale or remotely sensed classifications, there are many fine-scaled forest classifications based on the composition of species or species groups, rather than on the physiognomy of dominant species. For example, the US Department of Agriculture Forest Service forest type map includes 28 forest type groups in the United States, aggregated from 142 forest types associated with more than 900 tree species (Ruefenacht et al. 2008). Finer-scaled forest classification and mapping are useful for assessing patterns of disturbances, improving forest management and conservation, and estimating regional carbon budgets. However, due to their high resolution, such floristic classifications have been developed only at the subnational or national level (Thompson et al. 2012) and only rarely for the tropics, where high diversity makes floristic classification difficult.

3. WHAT MAKES FORESTS MORPHOLOGICALLY BIG OR SMALL?

3.1. Forest Structural Attributes and Climate Effects

Supplemental Material

Forests are three-dimensional and structurally complex systems and therefore comprise various vertical and horizontal structural elements (**Supplemental Table 1**; see the sidebar, Structural Features of Forest Stands). Traditionally, ecologists have measured the components of forest structure in relatively small sampling areas (McElhinny et al. 2005). Remote-sensing advances in recent decades have greatly improved our ability to measure a few critical variables of forest structure, such as leaf area and tree height, over large areas. Many studies show that the index

STRUCTURAL FEATURES OF FOREST STANDS

Forest structure is usually described by features or attributes of individual structural elements and spatial (horizontal and vertical) patterns of structural elements (Franklin et al. 2002). Individual structural elements such as leaf area, life form (deciduous or evergreen), branch arrangement, and soil depth can be critical for basic tree functions and competition for resources. Spatial patterns such as the size distribution of trees (dispersed or clumped), spatial distribution of biomass within a stand, canopy layers, and gaps may depict vegetation dynamics of a forest stand. Structural characteristics of trees, whether living or dead, together with other biotic and abiotic attributes form the underpinnings of forest ecosystem functioning and processes. The forest canopy is considered a particularly crucial constituent because it is the site of primary production and one of the principal functional interfaces between the forest and the atmosphere for exchanging carbon, water, and energy. Complex forest structures also give rise to diversified microclimates, niches, and habitats for maintaining the majority of terrestrial biodiversity.

of stand structural complexity measured by airborne light detection and ranging (LiDAR) is well correlated with field measurements, which suggests the possibility of using LiDAR more broadly to improve our understanding of forest structure globally (Kane et al. 2010, Næsset 2002).

Across a landscape, the perception of a morphologically big or small forest relies on the two most observable forest attributes: the height and density of canopy trees. The global percent tree canopy–cover map (**Figure 2*a***), based on data derived from the *MODIS* sensor, provides a horizontal view of tree canopy density at 500-m resolution (Hansen et al. 2003). A more recent map of global forest canopy height (**Figure 2*b***), using the first LiDAR data from a satellite sensor, GLAS, provides complementary vertical structure information (Lefsky 2010). Despite some uncertainties, the maps together provide some of the first global views of forest structure. They show that the densest forests occur in the high northern latitudes of Eurasia and North America, the tropical latitudes of the Amazon Basin of South America, the Congo Basin of West Central Africa, and insular Southeast Asia. The tallest forests occur in the same tropical regions and in some temperate coastal regions and remote mountain areas.

The first consistently derived, spatially explicit picture of the world's forests (see the sidebar, Where Are the World's Largest Forests?) supports ground-based observations by ecologists that forest biomass, high structural complexity, and biological diversity are concentrated where climate is wettest and warmest. It also demonstrates that boreal forests, although they may have a dense formation, are among the least complex and shortest forests in the world (**Table 1**).

Light detection and ranging (LiDAR): refers to sensors that emit laser pulses to measure the distance to forest canopies, intermediate layers, and ground level

Geoscience Laser Altimeter System (GLAS): the LiDAR instrument for continuous global observations of Earth

3.2. Forest Structure Development, Complexity, and Age

Disturbances are the main drivers altering forest structure, creating landscape mosaics, and setting the initial conditions for successional dynamics and structural development (Swanson et al. 2011). Structural development is often divided into several stages according to stand ages and structural complexity (Franklin et al. 2002). For instance, old stands are often marked by high levels of structural complexity due to horizontal diversification and processes that create and fill canopy gaps. Species diversity and tree-size variations contribute to structural complexity, which can be quantified using scores derived from multivariate analyses based on a comprehensive suite of structural attributes and geospatial data (McElhinny et al. 2005). The index approach is also used to link observed forest structural attributes with LiDAR data and high-resolution multispectral airborne imagery for mapping forest structural complexity or interpreting forest structural patterns with environmental variables (Kane et al. 2010, Pasher & King 2011). Remote sensing–based

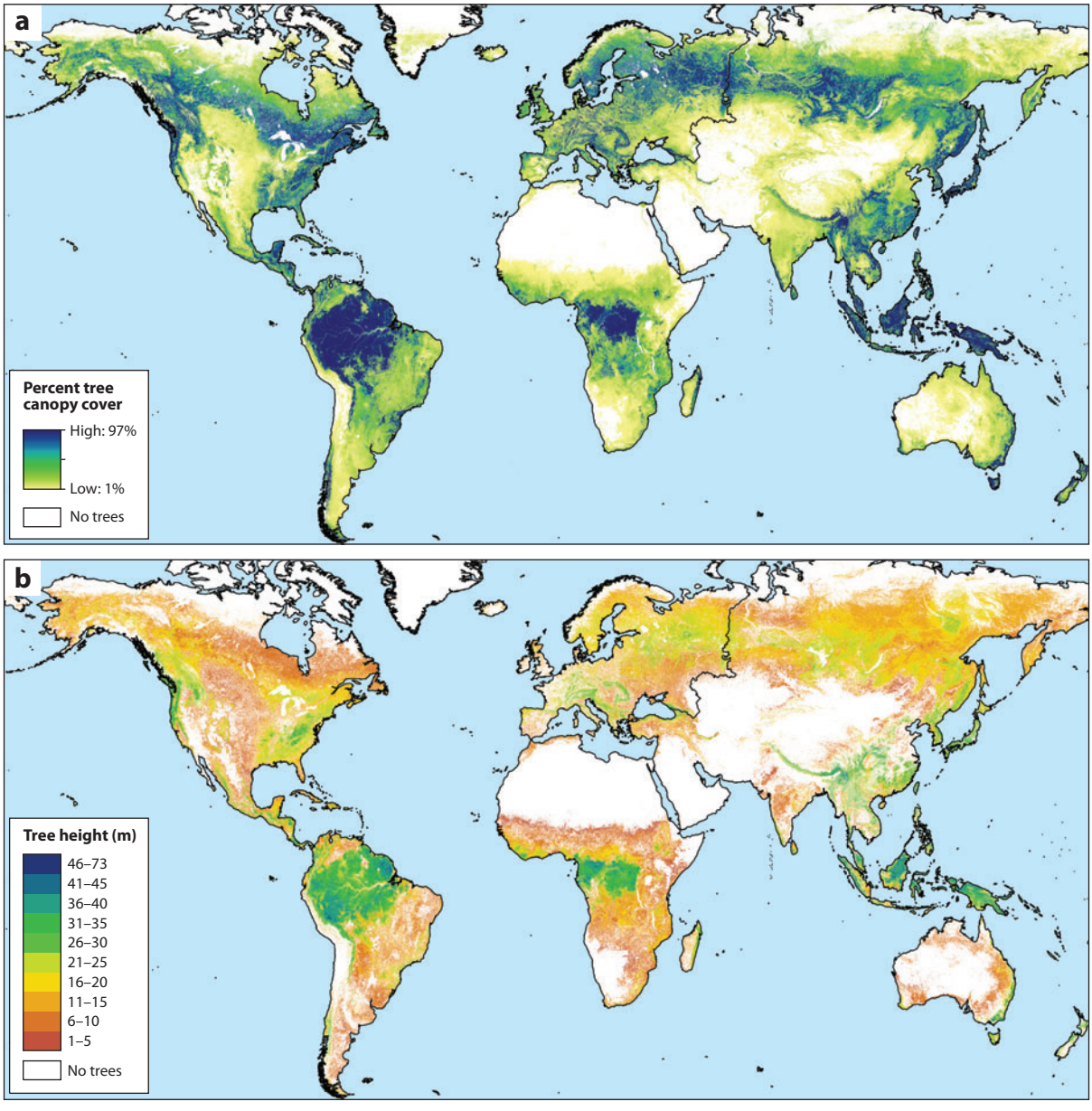

Figure 2

The structure of global forests. (*a*) Percent tree canopy cover (Hansen et al. 2003). (*b*) Global forest height (Lefsky 2010). The *MODIS*-based data are derived from seven bands designed for land-cover monitoring and spectral signatures of canopy reflectance.

WHERE ARE THE WORLD'S LARGEST FORESTS?

Tropical rainforests constitute by far the most extensive area of high-biomass forest. Yet, on a per unit area basis, the world's densest and tallest forests are temperate rainforests, stretching along the coastal margins of areas that include northwestern America, southern Chile, southeastern Australia and Tasmania, and New Zealand. These scarce forests occupy only 2–3% of the total temperate forest area. They occur near oceans and coastal mountains with cool summers, mild winters, and adequate precipitation all year, some of which may be in the form of coastal fog in areas with dry summers (Alaback 1991). As a result of long growing seasons and low rates of disturbance, these forests often feature huge and long-lived trees with the highest stock of living biomass and organic matter in the world (~500–2,500 Mg ha^{-1}). The most carbon-dense forest known is a eucalyptus forest in Australia that has an average carbon density of 2,844 Mg C ha^{-1}, of which 64% is in living aboveground biomass (Keith et al. 2009). However, compared with tropical rainforests, temperate rainforests have much lower species richness.

structural indices are used to identify successional stages, compare diversity of forest structures, and establish criteria for forest management and species conservation.

Forest age or time since the last disturbance is an important attribute of forest structure. Many deterministic processes during stand structural development, such as net primary production (NPP), mortality, biomass, and woody debris accumulation, are related to stand age (Spies 1998). Through a combination of forest inventory data, historical fire data, and satellite data (*SPOT4*-VEGETATION and *Landsat* TM/ETM) used to detect fire scars and forest harvests, the first continental forest age map of North America (excluding Mexico) was developed at 1-km and 250-m resolutions (**Figure 3**) (Pan et al. 2011b). Forest ages are relatively young in the southeastern United States and in parts of central Canada, reflecting the impacts of intensive industrial forestry practices and frequent natural disturbances, respectively. The oldest forests (>100 years), specifically old-growth temperate rainforests with high rainfall and little fire disturbance, are found primarily in the Pacific Northwest of North America (Pan et al. 2011b). The age distribution shows that, at least in boreal and temperate regions, most forests have been disturbed by natural causes, such as wildfires, or land management, over the past century. Although all forests are subject to some natural disturbances (and many are subject to human disturbances), disturbance frequency is likely to be inversely related to intensity. Within Amazonia, for example, a standard 1-ha plot is subject to some disturbance-caused mortality every year, but true stand-initiating disturbances occur only with return intervals measured in millennia or tens of millennia (Espírito-Santo et al. 2010).

Net primary production (NPP): the difference between GPP and plant autotrophic respiration and the source for growth and reproduction

***SPOT4*-VEGETATION:** an optical sensor aboard the fourth *SPOT* satellite providing daily global coverage of the land at a resolution of 1 km

***Landsat* TM/ETM:** Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM) are multispectral scanning radiometers carried aboard satellites for observing Earth's land and coastlines

3.3. Tree-Height, Biophysical, and Resource Limitations

Tree height is one of the most distinguishing features of forest structure. Canopy height can be detected relatively easily with remote-sensing radar and LiDAR (Shugart et al. 2010), and the maximum height of trees is closely related to total stand biomass (e.g., Feldpausch et al. 2012, Stegen et al. 2011). Several factors limit height growth in trees and, by extension, total forest biomass. Studies of the tallest trees in the world (e.g., *Sequoia sempervirens* and *Pseudotsuga menziesii*) appear to support the hydraulic limitation hypothesis (Ryan & Yoder 1997). Although the capillary forces that trees use to transport water are sufficient to overcome gravity and path-length resistance (Holbrook & Zwieniecki 2008), trees use different strategies to reduce water tension in conduits and to avoid the danger of embolisms. As a result, trees cannot always transport sufficient water from the soil to the top of trees, causing water stress and reduced stomatal conductance in the

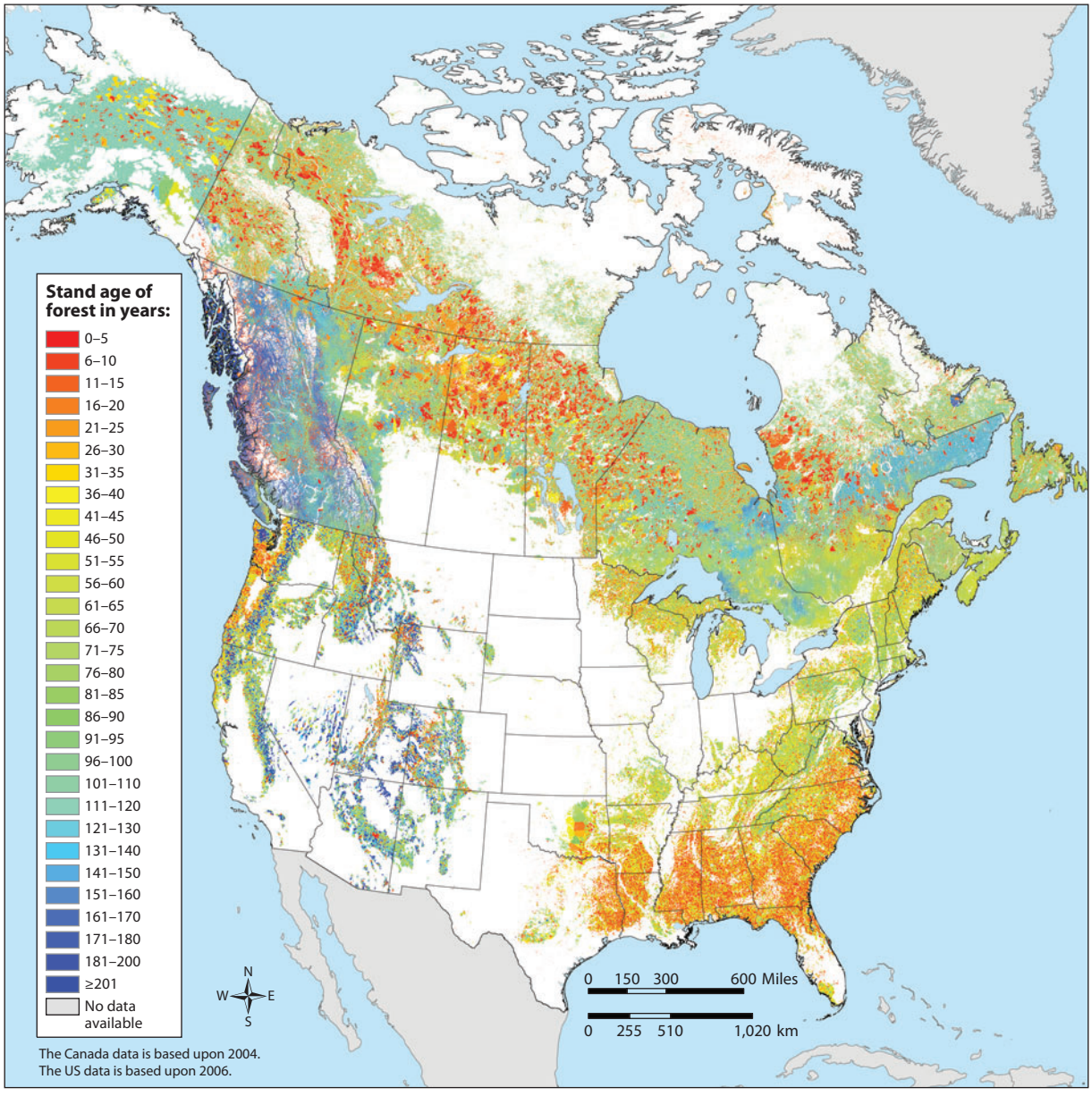

Figure 3

Forest age distribution in North America (excluding Mexico), developed by combining forest inventory data for the United States and Canada with several remote sensing–based disturbance data sources (updated from Pan et al. 2011b).

canopy. Such limitations may ultimately decrease carbon assimilation and height growth (Choat et al. 2012, Koch et al. 2004).

On the basis of the maximum drought stress that canopy leaf forms can sustain, the maximum height of redwoods was estimated theoretically to be 122–130 m (Koch et al. 2004). In practice, maximum tree height was found to be lower at drier sites (~80 m) and at sites with stronger storms

(~100 m). To resist mechanical failure induced by gravity and wind, the basal diameter of trees required for stability increases exponentially with height (King 2005); therefore, carbon investment costs to stem growth in taller trees will eventually limit tree height. Thus, both mechanical constraints and hydraulic factors limit the height growth of large trees (Niklas 2007). Other factors, including climate conditions and some trade-offs in tree growth strategies, may also restrict height growth. For instance, low temperature often restricts the rate of cell division in trees even when there is sufficient carbon supply; this finding may help explain why trees in boreal regions are shorter and grow more slowly even during the growing season (Rossi et al. 2007).

4. HOW IS BIOMASS AFFECTED BY ECOSYSTEM PROCESSES AND DYNAMICS?

4.1. The Global Relationship Between Forest Productivity and Biomass

Although forest biomass is partly limited by tree height, it is a complex property that integrates diverse functional processes and structural attributes, thereby linking forest productivity, basal area and height, and wood density. Forest biomass is driven ultimately by the long-term balance between the rate at which wood has been produced (growth) and the rate at which it has been lost (mortality). Likewise, biomass change, a key variable for understanding forest carbon budgets, results from imbalances between these growth and loss terms. Here, we examine the relationship between forest productivity and biomass, because most DGVMs estimate biomass simply as a cumulative function of NPP based on carbon allocation ratios to foliage, fine roots, and woody tissues (e.g., Sitch et al. 2008). In reality, the close linkage between stand-level productivity and biomass is less clear across many of the world's forests (Delbart et al. 2010, Keeling & Phillips 2007).

Early observations reported a linear relationship between aboveground NPP (ANPP) and aboveground biomass (AGB) on the basis of limited data from 25 forest stands in the continental United States (**Figure 4*a***) (Whittaker & Likens 1973). Through the use of findings from the International Biosphere Program and from newer tropical studies performed since the 1980s, more globally extensive and representative data sets have revealed that these two variables are not always linearly related (**Figure 4*a***) (O'Neill & De Angelis 1981) and sometimes are not even positively related (**Figure 4*b***) (Keeling & Phillips 2007). A few temperate rainforest sites have truly excessive AGB in relation to their ANPP (**Figure 4*b***); the longevity of dominant tree species makes exceptional contributions to their extraordinary heights and massive biomass (Mencuccini et al. 2005).

Globally, the AGB-ANPP relationship appears to saturate when ANPP values exceed 20 Mg ha^{-1} $year^{-1}$; these values are found primarily in tropical rainforests and seasonal forests (Keeling & Phillips 2007). Several mechanisms may contribute to this pattern. Compared with temperate deciduous forests, tropical forests can have lower carbon use efficiency (CUE, the ratio of NPP to GPP) (DeLucia et al. 2007), which results in a relatively smaller fraction of photosynthetic product being used for building biomass, even though tropical forests have generally higher productivity. Tropical forests can also be remarkably dynamic, with relatively high average biomass turnover and mortality rates (Phillips et al. 2004) that reduce the accumulation of living biomass (Quesada et al. 2012). Indeed, the average residence time of woody biomass across the moist tropics is estimated at only ~50 years (Galbraith et al. 2013), even though large canopy trees may live much longer (Martínez & Alvarez 1998). Biomass turnover rates in tropical forests are also highly variable across their complex landscapes (Martínez & Alvarez 1998, Quesada et al. 2012), further limiting the direct relationship between ANPP and AGB. Nevertheless, apart from the spatially restricted temperate rainforests, tropical forests still have, on average, the greatest biomass stocks

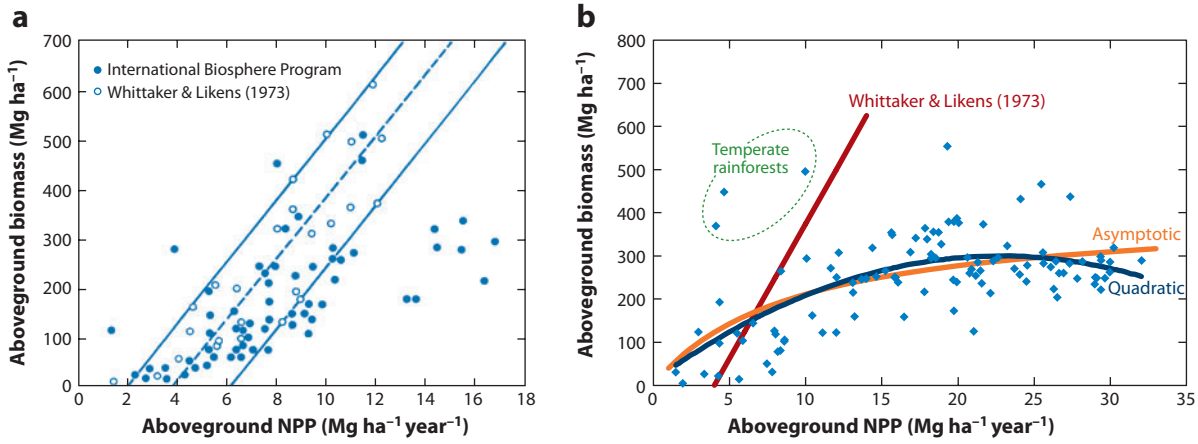

Figure 4

Relationship between forest aboveground net primary production (NPP) and aboveground biomass (AGB) for alternative data sets. (*a*) Relationship based on data from Whittaker & Likens (1973, *open circles*; *dashed line* shows regression fit and *solid lines* show data extremes) and the International Biosphere Program woodland data set (*solid circles*) (O'Neill & De Angelis 1981). (*b*) Data from original studies (panel *a*) with additional data from tropical lowland forests. The analysis uses the core data set of sites with a confidence index of ≥ 9 ($n = 106$) (Keeling & Phillips 2007). The red line represents the relationship from Whittaker & Likens (1973); the orange and dark blue lines are asymptotic and quadratic regressions for all data points; and the green dashed circle includes the data points from temperate rainforests (modified from Keeling & Phillips 2007, their figures 1 and 5b).

(Stegen et al. 2011) because of their moderate to high wood density (Baker et al. 2004), their high density of smaller trees (Feldpausch et al. 2012), and the disproportionate contribution of a small number of long-lived and large canopy and emergent trees (Stegen et al. 2011).

4.2. Macroecology, Edaphic Conditions, and Light Regimes

Even though there is a clear global influence of ANPP on AGB (**Figure 4*b***), the relationship between growth, mortality, and biomass has proven difficult to interpret universally because of nonlinear dynamics and the complexity of interacting environmental factors (Coomes & Allen 2007, Stephenson et al. 2011). For example, biogeographically there appears to be a strong positive relationship between forest NPP and mortality rates (Stephenson & van Mantgem 2005), but further investigation suggests that there is no direct causal relationship between them, because productivity and mortality result largely from different mechanisms (Stephenson et al. 2011).

On large regional scales it may be possible to disentangle the different drivers of growth, mortality, and biomass. For example, across the 6 million km^2 Amazon forest region, there is a coherent east-west gradient of multiple ecosystem properties (**Supplemental Figure 2**): Forests in the western Amazon Basin generally have higher productivity and mortality rates (higher turnover) but lower biomass and wood density and smaller trees compared with forests in the eastern Amazon Basin (Feldpausch et al. 2012, Phillips et al. 2008). Soil physical conditions in particular (rather than climate alone) have the strongest impacts on forest structure and dynamics in the Amazon Basin (Quesada et al. 2012). The western areas of the Amazon Basin near the Andes are characterized by soils that are newer and more fertile but have a marked tendency to be shallow, to be prone to waterlogging, and usually to have high bulk density in subsurface soil horizons. In contrast, the more weathered and chemically poorer soils of the east generally have a deeper structure and are better drained (Quesada et al. 2010). Forest dynamics in the western Amazon Basin are characterized by frequent disturbances interacting with shallow soils (e.g., greater vulnerability to

Supplemental Material

occasional drought or to wind disturbance), favoring faster-growing taxa with lower wood density; their greater susceptibility to disturbance provides a compositional feedback to help maintain a fast turnover system (Quesada et al. 2012). Forests in the central and eastern Amazon Basin, however, feature old-growth stands dominated by shade-tolerant species and taller trees with slower growth and lower mortality. Thus, although forests in Amazonia are mostly old growth, their ecosystem properties approximate a "successional" continuum along a landscape gradient that is triggered largely by edaphic factors. Within Amazonia, climatic variables such as mean annual temperature and rainfall seasonality appear to have only marginal effects on spatial patterns of biomass and productivity (Quesada et al. 2012).

Within forest communities, however, there is usually great variety in ecological behavior; growth and mortality rates of individual trees can be predicted in part from coherent sets of covarying leaf and wood traits that can specify rates of resource acquisition and loss (e.g., Dybzinski et al. 2011, Wright et al. 2004). For example, shade-tolerant trees with large leaf area–to–leaf mass ratios may respond opportunistically to increased levels of light and grow to large sizes because of their relatively fast growth rates and longevity (Fyllas et al. 2012). Many observations show that mortality is higher in small trees than in large trees, probably because of the suppressed growth in response to understory light environments (Stephenson et al. 2011), although the lowest mortality rate is often observed in midsized trees (Coomes & Allen 2007). Some observations indicate that mortality rates decrease with tree size within canopy species and increase with size within subcanopy species but that they generally increase from the top canopy layers to the lower layers (Bolhman & Pacala 2012).

4.3. Spatial Scale as a Factor in Emergent Ecological Properties

Although patterns and relationships among growth, mortality, and biomass can sometimes be complicated, spatial scale can help us interpret apparent differences in emergent ecological properties. At the global or continental scale, a positive relationship between NPP and mortality or turnover reflects broad-scale impacts of temperature and resource availability on forest productivity, biodiversity, and species interactions. For instance, compared with most temperate and boreal forests, tropical forests have both higher productivity and higher mortality rates but still maintain higher biomass (Larjavaara & Muller-Landau 2012, Stephenson & van Mantgem 2005). Thus, globally, the latitudinal pattern of faster carbon fixation tends to dominate the mortality term.

At the landscape level, forest attributes are also strongly influenced by disturbances, edaphic conditions, topography, and successional sequences (Franklin et al. 2002, Quesada et al. 2012). Early successional forests have a higher proportion of fast-growing species and higher mortality rates due to competition for light and growing space among trees and lower belowground allocation (Enquist & Niklas 2002), so they can have high woody productivity but still relatively low wood density and biomass. In contrast, forests in later successional or old-growth stages are often characterized by shade-tolerant species. These tree species may have relatively fast growth rates before reaching the canopy but often decreased biomass growth after canopy closure (Ryan et al. 2004). By maintaining slow growth and low mortality on relatively nutrient-poor soils, they may survive for many years and achieve a high biomass. Additionally, at the community scale, forests are a mix of tree species with different functional traits and growth behaviors in response to varying light, moisture, and nutrient regimes. The community-wide growth and mortality rates and their relationship to biomass are related to demographic properties but are also determined by the traits of dominant and canopy tree species (Strigul et al. 2008).

Given the complexity in ecological processes at different scales of organization, is there an approach to integrate relationships among growth, mortality, and biomass across all scales? Recent

advances in data-based theoretical research have given rise to an analytically tractable model of forest dynamics named the perfect plasticity approximation (PPA), which provides a framework for scaling up the traits or properties from individual trees to population, community, and ecosystem (Purves et al. 2008). The modeled results of growth and mortality rates, and the biomass changes of tree cohorts in temperate and tropical forests, were well validated by forest inventory data (Bolhman & Pacala 2012, Strigul et al. 2008). This model accurately predicted the composition of functional groups and diameter classes in the canopy and understory (Dybzinski et al. 2011), demonstrating that canopy- and height-structured competition for light is the most fundamental process driving forest dynamics and determining growth, mortality, and standing biomass of trees (Purves et al. 2008). When supported by high-resolution remote sensing of forest canopies such as LiDAR and aerial photography, the model has the advantage of simulating patterns of biomass and species turnover at landscape scales (Bolhman & Pacala 2012). Indeed, we anticipate that newer, similar models that can integrate ecological theory with data from ground-based forest inventories and remote sensing should eventually advance predictive understanding of forest carbon dynamics across scales, including forest structure, distribution, and functioning.

5. WHERE IS FOREST BIOMASS CONCENTRATED?

5.1. Productivity and Biomass Accumulation

Forest productivity is a major factor shaping the amount and distribution of terrestrial biomass (see **Supplemental Text 1**). Global terrestrial GPP is ~122 Pg C year^{-1}, 49% of which occurs in forests (**Table 2**). Other lands, including croplands, grasslands, and savannas, also have significant rates of GPP and NPP. Global NPP is estimated to be approximately half of global GPP, although CUE may vary among biomes (DeLucia et al. 2007). Over the whole year, the tropics have the highest biomass accumulation, followed by temperate and then boreal zones, although boreal forests appear to have very high NPP in their short growing seasons (**Figure 5*a*,*b***). Tropical forests account for two-thirds of all terrestrial biomass; temperate and boreal forests are significant, but each is equivalent to only ~20% of the tropical biomass (**Table 2**). Globally, forests account for 92% of all biomass; therefore, the distribution of forests is tantamount to the distribution of biomass.

Supplemental Material

5.2. Global Biomass Stock and Distribution

Paleoecological studies suggest that after the last glacial maximum ~18,000 years ago, global carbon storage in vegetation and soil roughly doubled (Adams et al. 1990). Biomass in natural vegetation peaked at ~770 Gt C during the preagricultural era ~10,000 years ago (Adams et al. 1990, Prentice et al. 2011). Current total biomass estimates are ~400 Gt C, based on global aggregation of forest inventories and field observations (**Table 2**). Human use of biomass products is largely responsible for the difference between actual and potential biomass globally. Haberl et al. (2007) and other authors have estimated that humans are currently responsible for removing ~16.3 Pg C year^{-1}—approximately 25% of global terrestrial NPP—for food and wood products, by land-use change, and human-caused fires. In addition, forest degradation, which lowers biomass density, has been significant globally, reducing the capacity of forests to provide goods and services. For instance, >850 million ha of tropical forests may already have been degraded by human activities (Blaser et al. 2011).

Human-caused reductions in forest biomass stocks differ across biomes (**Table 2**). In the temperate and boreal zones, where forests naturally occur, current forest biomass is only ~30% of

Table 2 Productivity and total biomass estimates for global terrestrial biomes[a]

Biome	Area[b] (10^6 ha)	GPP[c] (Pg C year^{-1})	NPP[d] (Pg C year^{-1})	Current biomass[e] (Pg C)	Potential biomass[f] (Pg C)
Tropical forest	1,949.4	40.8	21.9	262.1	352.0
Temperate forest	766.7	9.9	8.1	46.6	161.0
Boreal forest	1,135.2	8.3	2.6	53.9	180.0
Other land except cropland	7,870.0	47.8	25.9	20.0	79.0
Cropland	1,350.0	14.8	4.1	10.8	Not applicable
Total	13,071.3	121.6	62.6	393.4	772.0

[a]Based on data from Gough (2012) and other references; approximate date is 2005.
[b]Pan et al. (2011a) for forests; Beer et al. (2010) for other categories.
[c]Beer et al. (2010). GPP stands for gross primary production.
[d]Saugier et al. (2001). NPP stands for net primary production.
[e]Pan et al. (2011a) for forests (total biomass includes above- and belowground live biomass); IPCC (2006) and Ruesch & Gibbs (2008) for other categories.
[f]Prentice et al. (2011).

what the potential would be without human use of the land for food production, fiber, and other nonforest land uses. In contrast, the current biomass of tropical forests is still almost three-quarters of what would be expected in the absence of human influence. Countries in the temperate zone have followed a historical pattern of land-use change involving a gradual reduction in forest area and density as agriculture expanded, followed by a recovery of forest area and density to a level that is still lower than the preagricultural state (Kauppi et al. 2006). The early stages of this historical pattern of land-use change are already evident in the world's tropical countries, although future changes will not necessarily follow the same pattern that transpired in temperate forests.

Total live forest biomass of the world was recently estimated to be 363 Pg C; boreal forests have the lowest natural live biomass density and tropical intact forests the highest (**Table 3**). Globally, ~80% of live forest biomass is in aboveground tissues and ~20% is belowground (Cairns et al. 1997; Jackson et al. 1996, 1997). The highest proportions of belowground biomass are found in tropical deciduous and boreal forests (25% and 24%, respectively), whereas the lowest proportions are found in temperate coniferous and tropical evergreen forests (15% and 16%, respectively) (Jackson et al. 1996). Nonetheless, tropical evergreen forests typically have the highest root biomass densities of ~2.5 kg C m^{-2}, consistent with the high live biomass densities found there (Jackson et al. 1996, Pan et al. 2011a).

Although total forest biomass has been fairly stable since 1990, biome-specific changes reflect the status and trends of recent human use of biomass and environmental factors in different regions of Earth. The largest recent increase of live biomass density is for tropical regrowth forests, an expanding area where trees are regenerating after logging or nonforest land use. The live biomass density of both temperate and tropical forests is also increasing, probably because of a combination of factors that include continuing regrowth following abandonment from agricultural

Figure 5

(*a*) Global net primary production (NPP) estimated from *MODIS* satellite data for January 2012 and June 2012 (**http://neo.sci.gsfc.nasa.gov/**). (*b*) Global total biomass carbon density for the year 2000 (**http://cdiac.ornl.gov/**) (Ruesch & Gibbs 2008).

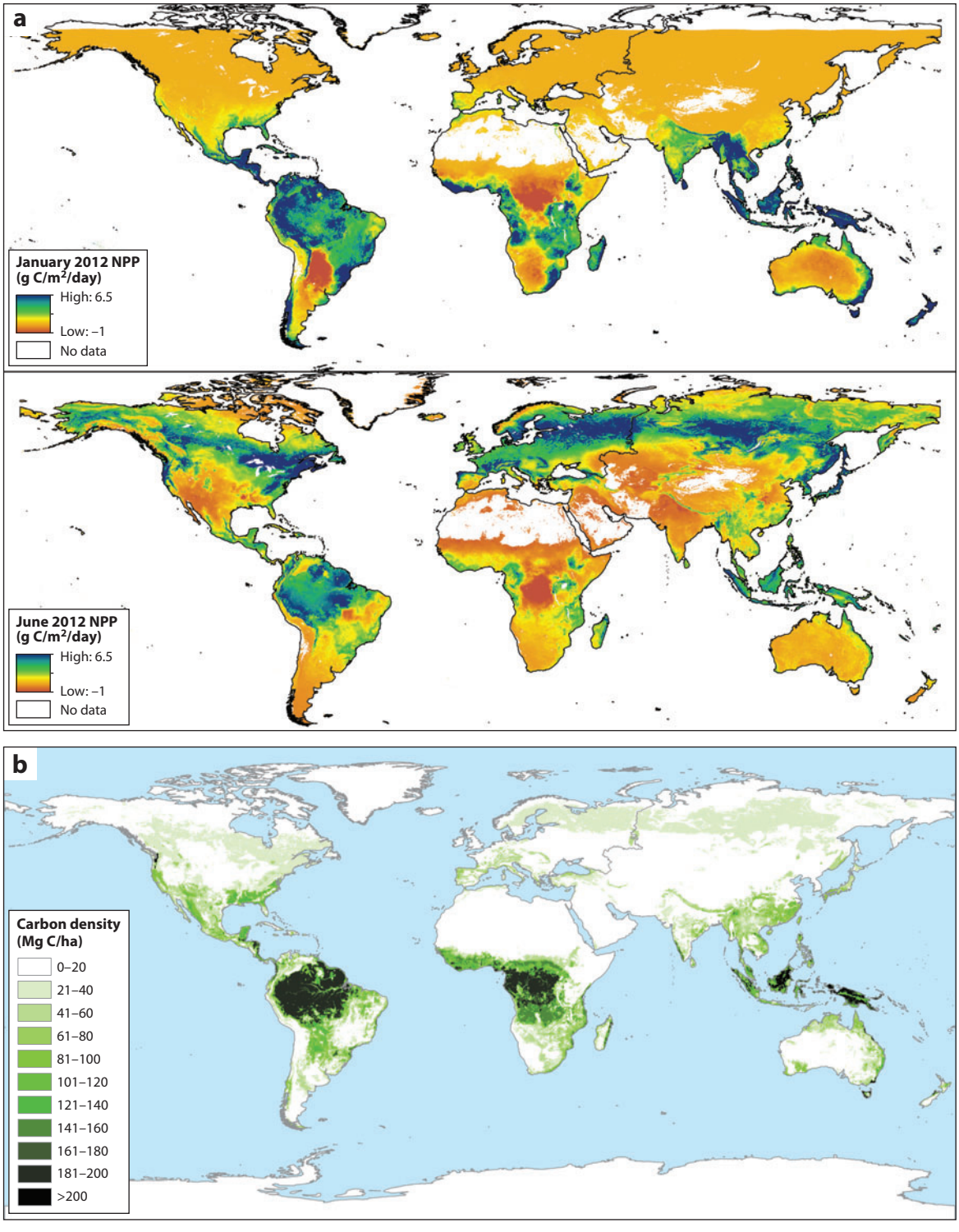
a
January 2012 NPP
(g C/m²/day)
High: 6.5
Low: –1
No data
June 2012 NPP
(g C/m²/day)
High: 6.5
Low: –1
No data
b
Carbon density
(Mg C/ha)
0–20
21–40
41–60
61–80
81–100
101–120
121–140
141–160
161–180
181–200
>200

Table 3 Forest carbon stock and carbon density by biome and year (Pan et al. 2011a)

Biome	1990		2007	
	Carbon stock (Pg C)	Carbon density (Mg C ha^{-1})	Carbon stock (Pg C)	Carbon density (Mg C ha^{-1})
Boreal				
Live biomass[a]	51.5	46.7	53.9	47.5
Necromass[b]	207.1	187.8	217.6	191.7
Total	258.6	234.5	271.5	239.2
Temperate				
Live biomass	40.3	55.0	46.6	60.7
Necromass	67.3	91.7	72.0	94.0
Total	107.6	146.7	118.6	154.7
Tropical intact[c]				
Live biomass	254.8	152.1	228.2	163.9
Necromass	196.2	117.0	165.1	118.6
Total	451.0	269.1	393.3	282.5
Tropical regrowth				
Live biomass	19.8	44.4	33.9	60.8
Necromass	31.1	69.4	43.8	78.6
Total	50.9	113.8	77.7	139.4
Global				
Live biomass	366.4	92.6	362.6	94.2
Necromass	501.7	125.6	498.5	129.4
Total	868.1	218.2	861.1	223.6

[a]Live biomass includes aboveground and belowground live biomass.
[b]Necromass includes organic matter in soils, litter, and deadwood.
[c]Total carbon stock in tropical intact forests in 2007 was lower than in 1990 due to lost forest areas from deforestation, whereas carbon density in the existing forests was still higher than in 1990.

use or logging and environmental influences such as nitrogen deposition, increasing atmospheric CO_2, and climate change (Pan et al. 2011a).

Globally, carbon in necromass (i.e., organic matter in soils, litter, and deadwood) is greater than in live biomass; it accounts for 58% of total ecosystem carbon (**Table 3**) and has an average density that is ~40% greater than that of live biomass. Forests are estimated to hold between 400 and 700 Pg C in the top 1 m of soil alone (Jobbágy & Jackson 2000, Pan et al. 2011a), a range that is caused in part by how forests are categorized globally. Boreal forests have significantly higher necromass than do other biomes. Tropical peatlands and mangrove ecosystems have the highest biomass density of forest ecosystems, the highest proportion of belowground biomass (roots), and the highest soil organic carbon stock. For example, mangrove forests in the Indo-Pacific region have more than 1,000 Mg C ha^{-1}, four times the average carbon density of the world's forests; the belowground proportion (roots and soils) accounts for 80% or more of the total (Donato et al. 2011).

5.3. Global Environmental Changes and Forest Biomass

Human-induced global environmental changes exert complex effects on forest productivity and carbon storage (Friedlingstein et al. 2006, Magnani et al. 2007). Some of the factors driving these changes are direct and physically alter forest areas and structures. For instance, tropical

deforestation, often through slash-and-burn agriculture, causes catastrophic destruction of vegetation structure and habitat and immediately releases a large of amount of the carbon stored in biomass as CO_2. Approximately 13% of the global anthropogenic carbon emissions between 2000 and 2010 resulted from tropical net deforestation emissions (Friedlingstein et al. 2010). However, other factors operate more sophisticatedly through tree physiology and other ecological processes; these include changes in climate (e.g., temperature, precipitation, and radiation) and atmospheric composition (e.g., CO_2, nitrogen deposition, O_3 and other pollutants) (Boisvenue & Running 2006, Lewis et al. 2009a). Different environmental changes often interact, as in the case of drought-induced forest diebacks, which change forest structure and morphology and interfere with carbon metabolism and dynamics (Walther 2010).

Recent climate warming has been most severe at higher latitudes (Christensen et al. 2007), causing increases in the frequency and intensity of wildfires and insect outbreaks in boreal forests (Flannigan et al. 2005, Kurz et al. 2008, Shvidenko et al. 2008). The higher mortality has, at least temporarily, increased the mass of deadwood in boreal forests (Pan et al. 2011a). Long-term data from forests unaffected by wildfires or insects in Canada showed that warming-induced drought stress also increased annual tree mortality from less than 0.5% of biomass in the early 1970s to ~1.8% more recently, and decreased biomass accumulation in western Canada, where moisture deficiency was greater (Peng et al. 2011). In contrast, the boreal forests of Eurasia have increased tree growth by ~0.3% to 0.4% per year on average since the 1960s, thereby increasing biomass stocks, despite increased mortality due to disturbances. This trend is probably related not to management or disturbance regimes but rather to a long-term change in environment such as a climate trend or CO_2 fertilization (Shvidenko et al. 2008).

Tropical forests of the Amazon and Africa have shown concerted increases in stem turnover and carbon dynamics over the past few decades (Phillips et al. 2009, Lewis et al. 2009b). Evidence from extensive in situ monitoring networks indicates recent increases in biomass of old-growth forests over coarse spatial scales and decadal timescales (Lewis et al. 2009a, Phillips et al. 2008), perhaps driven by CO_2 fertilization and other increases in resource availability. An earlier projection suggesting large-scale dieback for Amazonia within 50 years (Cox et al. 2000) has been reversed, with strong indications of future increases in productivity and biomass (Huntingford et al. 2013, Ramming et al. 2010). Recent analyses even suggest potential increases in forest area in the event that deforestation and degradation are controlled, as the climate zone theoretically suitable for tropical forests may expand outward from the equator (Zelazowski et al. 2011). Nevertheless, there is recent on-the-ground evidence of tropical forest vulnerability to changes in climate variability and extreme droughts, at least in some places. For example, in the Amazon Basin, two major droughts (one in 2005 and the other in 2010) occurred within an unusually short period of time and killed enough trees to eliminate at least 10% of the additional biomass that had accumulated over the previous two decades (Lewis et al. 2011, Phillips et al. 2009). In a few locations in Central America and Southeast Asia, decreasing growth rates have recently been reported and have been linked to high temperatures that may cause autotrophic respiration rates to exceed photosynthesis (e.g., Wood et al. 2012).

In temperate forests, both remote-sensing and forest inventory data have shown increases in forest productivity and biomass densities in recent decades (e.g., Nemani et al. 2003, Pacala et al. 2001). The increases were largely a response to forest management and land-use dynamics such as forest recovery from abandoned agriculture or changes in forest age structures toward more productive stages (Ciais et al. 2008, Houghton 2007). Evidence from biogeochemical process models suggests that climate change, elevated CO_2, and nitrogen deposition have also affected forest productivity and biomass stocks. In general, nitrogen deposition appears to have a more positive effect on NPP than on other factors in temperate forests, although the positive effect

from elevated atmospheric CO_2 is also significant; climate changes have less obvious effects on average productivity except for increasing the interannual variability (Magnani et al. 2007, Pan et al. 2009). Climate-induced drought and heat stress and associated insect outbreaks and wildfires have also affected some temperate forests, particularly those in relatively arid regions such as the western United States, which has had increased tree mortality, suppressed forest productivity, and reduced forest biomass and total carbon stocks (Allen et al. 2010, van Mantgem et al. 2009).

Despite widespread reports of increased mortality and deadwood mass, established forests around the world have shown consistent increases in biomass and total carbon density (including stocks of biomass, deadwood, litter, and soils) (Pan et al. 2011a). This finding suggests that, overall, conditions must have favored increased wood production and imply a global driver such as elevated CO_2 as one plausible mechanism enhancing biomass gains (Lewis et al. 2009a), as has been predicted from theoretical considerations (Lloyd & Farquhar 1996). It will be particularly important to understand this new era of accelerated forest carbon production and loss, as well as how such changed dynamics will affect forest biomass stocks, forest structure and distribution, and future trajectories.

5.4. Improving Knowledge of Forest Biomass by Advancing Approaches

With rapidly changing forest dynamics owing to climate change and anthropogenic impacts, improved monitoring of biomass changes and understanding of the causes of changes will be necessary to sustain and enhance important ecosystem services of forests. Here, we discuss how anticipated advances in remote sensing, field measurements, and analysis methods can keep pace with the increasing demands for information to support policy and management decisions.

Supplemental Material

5.4.1. Expanding approaches for estimating biomass. Estimating and mapping forest biomass (**Supplemental Text 2**) usually involve a combination of two or more of the following methods: remote sensing, field measurements, and modeling, often tied together in a GIS framework for producing maps at various scales. Several new global initiatives to improve forest monitoring from space and on the ground are under way (e.g., Global Observation of Forest and Land Cover Dynamics; **http://www.fao.org/gtos/gofc-gold/index.html**).

Advanced uses of ground-based LiDAR are in their infancy. In addition to the use of ground-based LiDAR for in situ biomass estimation, some future applications may include assessment of interactions between light and tree canopies, microhabitats, and absorption of photosynthetically active radiation (Dassot et al. 2011). When fully developed, these new LiDAR techniques could be widely deployed to greatly improve knowledge of vegetation structure and ecosystem processes, with fine-scale details at many field sites around the world.

Expanded networks of in situ monitoring sites are especially needed in the undersampled tropical forests of the world (Havemann 2009). Leading networks include RAINFOR, which focuses on ecosystem function and long-term biomass dynamics across Amazon forests; AfriTRON (African Tropical Rainforest Observation Network, a sister network of RAINFOR in South America), which currently spans 10 countries across tropical Africa and has similar aims; the Center for Tropical Forest Science (CTFS) network, whose aims include understanding long-term population dynamics in large tropical plots; and the Global Ecosystem Monitoring network, which aims to measure and understand ecosystem functions and traits at high temporal resolution (Marthews et al. 2012). However, the biome is huge, tropical forests are very diverse, and the potential drivers of change are complex. Thus the combined current sampling effort is considered inadequate for

accurately tracking and understanding change across tropical forests (St. James's Palace Memorandum on Tropical Forest Science 2013).

Amazon Forest Inventory Network (RAINFOR): an international collaboration that aims to understand the ecological dynamics of Amazon ecosystems

The Center for Tropical Forest Science (CTFS): a global network of forest research plots and scientists dedicated to the study of tropical and temperate forest function and diversity

5.4.2. Cutting-edge remote-sensing technologies. After more than 30 years, the medium-resolution passive optical sensors on *Landsat* satellites have compiled the longest running time series of remotely sensed digital images of Earth (Cohen & Goward 2004). *Landsat* data have been frequently used at regional and continental scales for classifying vegetation and for assessing attributes such as percent forest cover, leaf area index, and disturbances, which are key variables for spatial ecosystem models and for estimating biomass. Spectral attributes of vegetation are related to biomass and can be used with field data and models to provide relatively accurate and spatially explicit estimates over large areas. For example, Kellendorfer et al. (2012) developed one of the first high-resolution (30-m) baseline estimates of canopy height, aboveground live biomass, and standing carbon stock for the conterminous United States.

Like *Landsat*, the *MODIS* satellite has provided useful information about ecosystems, particularly regarding productivity and large-scale disturbances (e.g., Running et al. 2009, Wang & D'Sa 2010). *MODIS* has a coarser spatial resolution than that of *Landsat*, but its daily temporal resolution yields more cloud-free images, so it is particularly useful for generating global products (**Figures 1**, **2**, and **5**). Both *Landsat* and *MODIS* signals "saturate" at higher leaf area densities, meaning that the passive optical signal cannot differentiate between ecosystems with moderate to high levels of biomass (Sanchez-Azofeifa et al. 2009). Coarse-resolution optical sensors are also limited in their ability to detect early secondary vegetation regrowth and small disturbances that remove individual trees.

High-resolution optical sensors such as Rapideye, aerial photographs, and active remote sensors can overcome many of the limitations of *Landsat* and *MODIS* for monitoring individual trees or small disturbances. These high-resolution sensors have historically been limited in spatial coverage because of their high cost and the volume of data generated. Synthetic aperture radar has the distinct advantage of penetrating clouds that mask Earth from optical sensors and, like LiDAR, can provide information about vegetation height and structure. Both LiDAR and radar sensors can accurately measure vegetation height, do not saturate as quickly as optical sensors under high biomass conditions, and can be effective at estimating and mapping biomass at fine scales (Asner et al. 2012, Goetz & Dubayah 2011).

5.4.3. Integrating spectral monitoring systems and field observation networks. Combining remote-sensing measurements with on-the-ground data should drive improvements in the next generation of maps of forest biomass and function. Both approaches have limitations. Field measurements can sample only a small fraction of the global domain, whereas remote-sensing techniques suffer from limitations imposed by varying sensor angles, atmospheric properties, physical constraints, and technological change. Thus, the great advantages of remote sensing, such as uniform measurements across the full domain, need to be combined with the strengths of field measurements, including detailed measurement of tree biomass and species and ground-based tracking of growth and mortality through time. Recent investigations of landscape-scale and larger-area estimates of forest biomass have attempted to explicitly integrate LiDAR with field validation plots by using allometric height-biomass relationships (e.g., Asner et al. 2012, Saatchi et al. 2011).

There is much room for improvement when scaling up to continent- and biome-scale estimates from emerging precise, locally replicated measurements, such as those from tropical plot measurement networks (e.g., Lewis et al. 2009b, Phillips et al. 2009). These efforts will clearly

benefit from the more sophisticated maps of forest area and other attributes becoming available from remote sensing. New indirect observation techniques can also help estimate biomass change or productivity. For example, an inversion approach based on measurements of atmospheric CO_2 concentrations may yield reasonable estimates of productivity for very large areas (Gurney & Eckels 2011), but the lack of terrestrial CO_2 records in the tropics greatly limits the ability to constrain tropical carbon budgets. New efforts to establish such measurements from satellites or via repeated sampling from small aircraft above remote forest regions promise to provide the requisite top-down constraints on estimating total carbon fluxes over large areas (Gloor et al. 2012).

Plant functional types (PFTs): classifications of species that show similarities in growth forms and their responses to environmental conditions

5.4.4. Enhancing dynamic global vegetation models. DGVMs are the only existing class of models that can simulate simultaneously global vegetation distributions and feedbacks of carbon and water exchanges to the atmosphere under different climate scenarios (e.g., Cramer et al. 2001, Sitch et al. 2008). DGVMs are useful tools for diagnosing the potential responses of forest NPP and biomass to changing climate and atmospheric composition, such as rising CO_2 concentration (Lewis et al. 2009a). For instance, the use of DGVMs has suggested that the efficiency of forest carbon uptake under future climate change will decrease, with forests becoming less capable of mitigating the growth in atmospheric CO_2 concentrations (Friedlingstein et al. 2006).

Current DGVMs still have significant uncertainties for simulating forest biomass and carbon dynamics. The uncertainties are partly due to unrealistic forest dynamics represented by plant functional types (PFTs) (Purves & Pacala 2008). In the future, DGVMs may evolve to include the effects of changes in species composition and height-structured competition within PFTs, adopting an approach similar to that emerging in the new class of PPA models discussed above. Linking DGVMs with high-resolution remote-sensing data of vegetation structure and species composition should enhance predictions of forest dynamics, changes in forest carbon storage, and feedbacks in climate systems.

SUMMARY POINTS

1. Climate is the primary determinant of forest distribution at global and continental scales, but at the scales of landscapes and stands, it is topography, soil, species interactions, and disturbance that define additional complexity in forest assemblages and structures.
2. Advanced remote-sensing technologies have revealed great discrepancies between actual forests and their potential distributions, particularly in temperate zones, reflecting the extent of anthropogenic alteration of forest landscapes and human biomass use.
3. Relationships among forest productivity, biomass, and tree mortality vary and are scale dependent, given that different mechanisms or environmental factors dominate at different scales.
4. Relative to the preagricultural era, only approximately half of the Earth's live terrestrial biomass remains, much of it concentrated in the tropical lowlands. Global deforestation and forest degradation have been extensive, causing the loss of biomass and increased carbon emissions.

5. Over the past two decades, established forests around the world have shown consistent increases in biomass density and in total carbon density, despite increased mortality in some regions. This trend suggests that, overall, conditions are favorable for increasing biomass stocks in forests and wood production, implying a single global driver or linked set of drivers as plausible mechanisms enhancing biomass gains. Global forests appear to have become more dynamic under today's changing environments.
6. Climate change and land-use change will continue to be dominant factors shaping forests and their functions in the coming decades. Throughout this review, we attempt to summarize the current understanding of the world's forests and how they have been shaped over time in an effort to highlight their irreplaceable services to humanity.

FUTURE ISSUES

1. Global-scale tools will be increasingly powerful for analyzing important ecological issues, yet we still lack some critical monitoring infrastructure as well as the capacity to fully utilize the information that could be provided. For example, the benefits of large-scale three-dimensional imaging for mapping forest structure are well documented, but at present there is no satellite system delivering this information. Currently planned missions for orbiting laser altimeters will enhance our ability to map and monitor dynamics in forest structure. Space-based hyperspectral sampling would also potentially improve our understanding of forest canopy composition, chemistry, and function.
2. We reiterate the importance of improving ground-based monitoring networks, including to calibrate and validate the increasing flow of remotely sensed data. Robust, standardized networks of field monitoring sites to complement global satellite observations are still lacking, particularly in tropical forests, where most of the biomass and species reside. Many countries lack sufficient technical capacity to participate in global networks and analyses. Where such networks already exist, they are providing increasingly vital information about forest processes and the abundance of critical ecosystem services provided by forests, including the production of food, fiber, timber, medicine, and clean water.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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