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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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The global distribution of net primary production: resolving the paradox

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Abstract. The distribution of the diversity and abundance of life on Earth is thought to be shaped by the patterns of plant growth (net primary production, NPP) in the oceans and on land. The well-known latitudinal gradient of species diversity reaches its maximum in tropical rain forests, which are considered to be the most productive ecosystems on the planet. However, this high tropical productivity on land is the opposite of the well-documented distribution of marine productivity, which is greatest in the high-latitude oceans around the poles. This paradox can be resolved by a reevaluation of the terrestrial productivity gradient. Compilations of direct measurements of forest NPP show that annual NPP in tropical forests is no different than annual NPP in temperate forests, contrary to recent syntheses and to the output of global vegetation models. Other properties of forest ecosystems, such as basal area of trees, wood density, and the ratio of wood to leaf production, as well as animal properties such as body size, population density, and reproductive rates, support the conclusion that ecologically relevant terrestrial productivity is actually highest in the temperate latitudes, reaching a maximum between 30° and 50° before declining toward the poles. This "reversal" of the latitudinal productivity gradient, if substantiated by a systematic global sampling effort, will necessitate a major reevaluation of ecological and evolutionary theory, as well as conservation strategies and international development policies.

Key words: biomass; forest; gradients; latitude; marine; net primary production; NPP; secondary production; species diversity; terrestrial.

Introduction

Net primary production, the rate at which plants convert carbon dioxide and water into energy-rich carbon compounds, is the foundation for all life on Earth. Appropriate management of the Earth's net primary production (NPP) is critical for stabilizing and eventually reducing the atmospheric concentration of carbon dioxide (IPCC 2007). However, the importance of understanding the total amount and accumulation rate of plant carbon goes beyond current issues of atmospheric chemistry and climate change. The global pattern of plant biomass and biomass production is the template that has shaped the evolution of life on Earth. Assumptions about the global pattern of productivity have also shaped many aspects of ecological and evolutionary theory, particularly those related to biodiversity, speciation, population dynamics, resilience, rarity, and conservation. The latitudinal gradient of increasing biodiversity from temperate to tropical regions is thought to be at least partially the consequence of a parallel gradient of increasing plant productivity from temperate to tropical regions (Connell and Orias 1964, Pianka 1966, Rohde 1992, Hawkins et al. 2003, Willig et al. 2003, Hillebrand 2004). Accurate information on these patterns is essential for understanding the causes of variation in the Earth's biodiversity, as well as for the conservation and sustainable management of natural resources, including the Earth's climate.

However, two widely accepted facts about the spatial distribution of net primary production (NPP) by plants over the Earth's surface are in direct conflict. The pattern of marine NPP, which is well-known from fisheries records and confirmed by satellite images of algal chlorophyll, is that the highest productivity is in the high latitudes, particularly in the northern hemisphere, with declining NPP toward the equator, and

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obvious variation from river outflows and current upwellings (Fig. 1A). The pattern of terrestrial NPP, based on multiple syntheses and confirmed by satellite images and sophisticated computer models of global vegetation, is the opposite of the marine pattern, being greatest in tropical rain forests along the equator and declining toward the temperate regions to the north or south (Westlake 1963, Leith and Whittaker 1975, Ajtay et al. 1979, Olson et al. 1983, Field et al. 1998, Saugier et al. 2001) (Fig. 1B). While this paradox is rarely discussed, our understanding of the Earth's atmosphere, ecology, evolution, and biogeochemical processes cannot be complete until we are able to explain the opposing patterns of marine and terrestrial productivity, and their apparently opposing effects on ecological and evolutionary processes, since both marine and terrestrial diversity are highest in the tropics.

How do the factors that drive NPP differ between marine and terrestrial ecosystems? Because the basic processes of plant photosynthesis are the same for terrestrial and marine/aquatic plants, the key factors must be the physical and chemical properties of the environments in which plant growth occurs, or the carbon allocation and life history dynamics of the plants themselves.

Two types of information can potentially help explain and resolve these conflicting patterns: (1) measurements and estimates of NPP in terrestrial and marine systems that are as direct and simple as possible; and (2) global patterns of the availability of critical plant resources in terrestrial and marine systems. A third type of information, about the properties of plants and animals that are expected to affect or be affected by NPP, can potentially support or contradict hypotheses about the spatial patterns of NPP. Examination of these three bodies of information, discussed below, leads to the conclusion that there should be no conflict between the marine and terrestrial patterns of NPP, and that one of the commonly accepted patterns is wrong. The information we have compiled suggests that it is the terrestrial pattern that is incorrectly understood, and the true terrestrial gradient of NPP is actually consistent with the marine pattern, and thus is the opposite of the current dogma.

Because the information for the marine patterns of NPP is unequivocal, we will begin with an examination of marine patterns, and then proceed to the terrestrial patterns and a discussion of the data and models used to estimate the pattern of terrestrial NPP.

Patterns of Marine NPP and Nutrients

Marine NPP was a major driver of the preindustrial cultures and economies of civilizations in the higher latitudes, and is still a major driver of the global fishing industry (Simonstad et al. 1978, Valavanis et al. 2004). While many fisheries have been depleted, they are typically replaced by a fishery based on a lower trophic level that is often more productive than the original fishery, consistent with ecological theories of trophic dynamics (Pauly et al. 1998, Myers and Worm 2003). It is clearly the very high NPP produced by marine phytoplankton (e.g., Behrenfeld et al. 2001) and picoplankton (Richardson and Jackson 2007) in the cold oceans, particularly in the northern hemisphere (Fig. 2), that supports both the fisheries and the high densities of marine fish, birds, and mammals that breed in the Arctic and, to a lesser degree, the Antarctic (Pauly and Christensen 1995, Stevick et al. 2002).

The most consistent large scale data on the spatial patterns of marine NPP come from the Sea-viewing Wide Field-of-view Sensor (SeaWIFS) satellites, which have been operational since 1997. These sensors detect light reflected from chlorophyll (contained in phytoplankton and picoplankton) in seawater, providing a standardized estimate of the amount of chlorophyll supporting photosynthesis up to a depth of approximately 30 m in marine waters (O'Reilly et al. 1998, Siegel et al. 2002, Hyde et al. 2007). The conversion of chlorophyll *a* values to NPP has proven to be complex, and there are a number of different algorithms that produce somewhat different NPP values (Laws et al. 2000, Behrenfeld et al. 2001, 2006, Marra et al. 2003). However, all of the marine estimates are highly correlated with the chlorophyll a values (e.g., Fig. 1A) upon which they are based. There are obviously strong seasonal variations in temperature, day length, ice cover and thus marine NPP at the high latitudes (Fig. 2), as well as some variation from year to year. The long-term average of all SeaWIFS images from 1997 to 2007 provides a reasonable picture of the annual average spatial variation in algal chlorophyll *a*, and by inference, average marine NPP across the planet (Fig. 1A).

Inspection of the global distribution of marine/aquatic chlorophyll *a* (Fig. 1A) emphasizes that marine and freshwater productivity is driven by nutrients derived from the continental land masses, in the form of dissolved and suspended minerals in surface waters, as well as minerals mobilized by upwellings from terrestrially derived marine sediments (Hatcher and Segar 1976, Sarmiento et al. 2004). The extensive coastline and river runoff of the high-latitude North American and Eurasian land masses clearly support the high primary and secondary productivity of the adjacent continental shelves and northern oceans. The effects of the outflows of the Ob and Yena Rivers, as well as the other rivers that drain Siberia toward the north, are conspicuous, as is the outflow of the McKenzie River that drains the Northwest Territories of Canada. Around the world, the effects of the outflows of major rivers are apparent, including the Mississippi, Amazon, Parana, Congo, Tigris and Euphrates, Indus, Ganges, Irrawaddy, Yangtze, and Huang. Also notable is the high average concentrations of chlorophyll *a* in the northern lakes of North America and Eurasia, as well as the equatorial lakes in the volcanic plateau of Africa, which are surrounded by fertile soils (note, however,

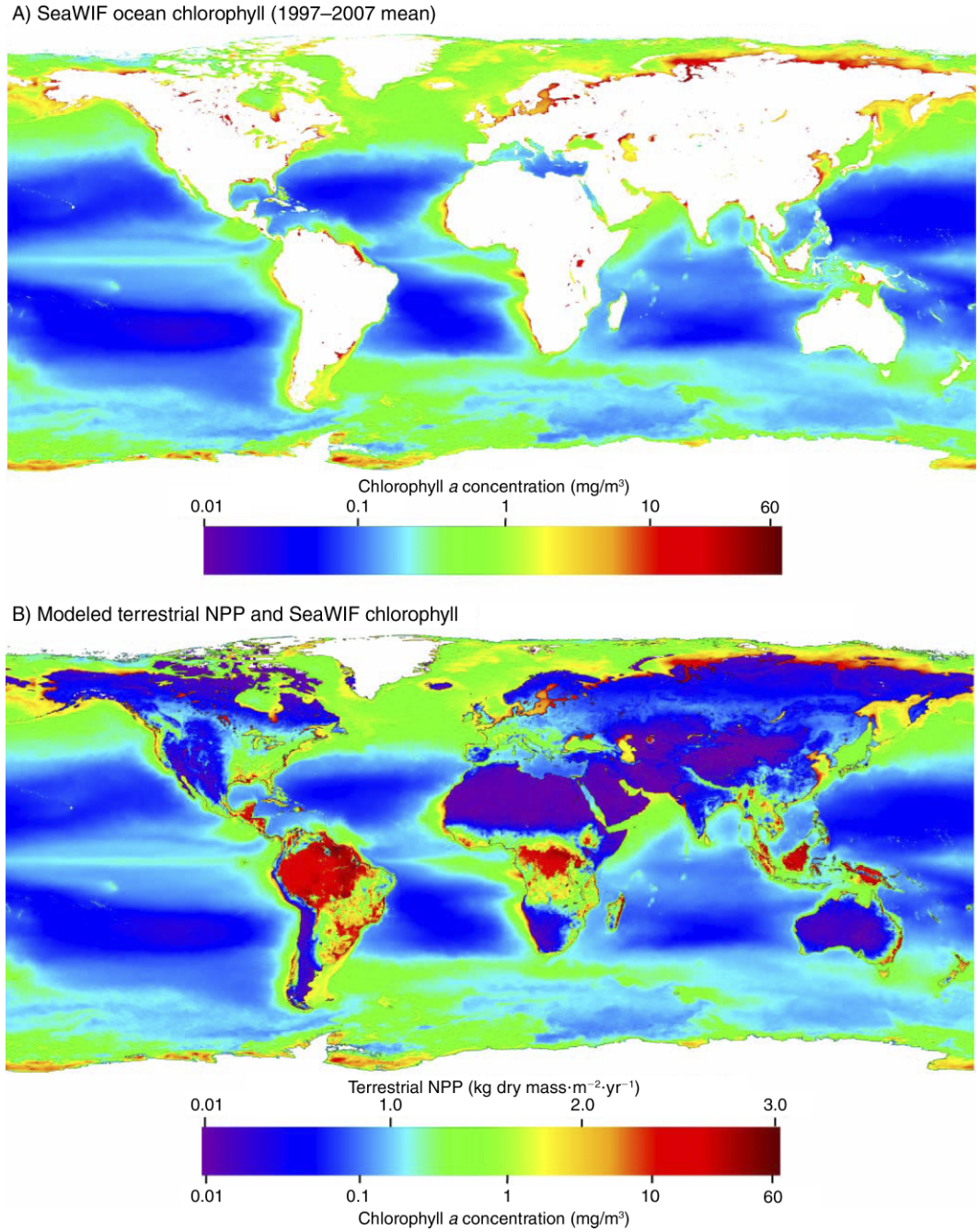

FIG. 1. Global distribution of marine and terrestrial net primary production (NPP, annual totals). (A) Ocean surface (to 30 m depth) chlorophyll *a* concentration, 1997–2007 mean values from SeaWIFS satellite. Ocean chlorophyll *a* concentration is highly correlated with NPP. (B) Terrestrial NPP, generated by the Carnegie Ames Stanford Approach carbon model (Field et al. 1998, Imhoff et al. 2004), superimposed on ocean chlorophyll *a* for reference.

that the SeaWIF sensors are calibrated for the oceans, not for the generally shallower and potentially sediment-rich freshwater bodies).

The nutrient content of terrestrial runoff clearly influences the productivity of the adjacent marine ecosystems, particularly the continental shelves. Phosphorus, iron, and silica are among the elements that have been identified as limiting marine NPP in various parts of the world's oceans (Black and Shimmield 2003), and are supplied by the dissolution and transport of terrestrial minerals, carried by rivers and dust storms (e.g., Smith and Demaster 1996, Bishop et al. 2002). The nutrient content of high-latitude soils, which have been exposed to cycles of glaciation that expose and pulverize

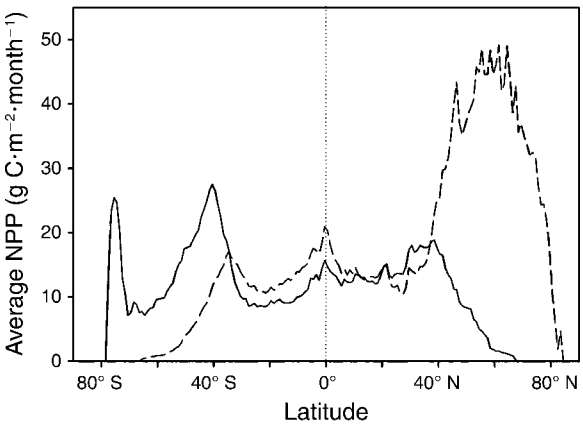

FIG. 2. Seasonal changes in the latitudinal distribution of ocean NPP for the three-year SeaWIFS record. The solid line is the average Austral summer (December through February) NPP; the dashed line is the average Boreal summer (June through August) NPP. (The figure is from Behrenfeld et al. [2001]; reprinted with permission of AAAS.)

fresh minerals, is typically much greater than that of tropical soils, which are exposed to much warmer temperatures that accelerate mineral weathering, and also to high precipitation, which leaches nutrients out of the soil (Sanchez 1976, Brady and Weil 2002). As a consequence, the heavily weathered soils of the tropics are known to be much lower in critical plant nutrients, such as available forms of phosphorus, as well as cations such as K, Ca, Mg, and Mn and other micronutrients, but are often high in Fe, Al, and total P, while low in available P (Sanchez 1976). The nutrient deficiency of the soils of the lowland tropics must be part of the explanation for the lower productivity of the tropical intertidal zone and continental shelf, particularly near South America and Africa, in areas of abundant precipitation and runoff.

The ancient continent of Australia confirms the importance of terrestrially derived nutrients for marine productivity. The soils of Australia, a heavily eroded and weathered land mass with little significant orogenic activity in the past 300 million years, are among the most infertile soils in the world (McKenzie et al. 2004). In addition, the arid climate of temperate Australia produces very little runoff, particularly along the southern coast, at latitudes similar to those with much greater marine productivity in North America, Eurasia, South America, Africa, and New Zealand (Fig. 1A). Similarly, the arid conditions around much of the Mediterranean Sea, particularly the southern shore, provide very little nutrient inflow, leading to low productivity. The contrast between the northern oceans and the southern ocean (Figs. 1A and 2), which has no significant mid- and high-latitude land mass, confirms the major role of terrestrial runoff in driving marine productivity.

A critical issue for understanding the distribution of marine NPP is the role of surface and subsurface currents in redistributing nutrients derived from terrestrial erosion. While the terrestrial source of the high marine productivity in the northern latitudes is obvious, it is less evident what drives the high-productivity zones near Antarctica. Runoff from the Antarctic land mass, at least until recently, is minimal, and most glacial runoff is frozen into ice at the continental margins (Vaughan 2006).

Somewhat surprisingly, much of the productivity of the Southern Ocean is actually driven by nutrients supplied by slow, deep currents from the high latitudes of the northern hemisphere. The North Atlantic Deep Water (NADW) is a slow-moving, cold, dense layer of nutrient-rich water that takes approximately 300 years to travel from the North Atlantic to Antarctica, where it is forced to the surface by the colder Antarctic deep waters and mixes with the Antarctic Circumpolar Current (Open University Course Team 2001:222). This North Atlantic water drives some of the productivity that supports the whales, penguins, and seabirds that feed in the Southern Ocean (Trujillo and Thurman 2005:398). Some of this North Atlantic water spreads northward again as Subantarctic Mode Water at the depth of the thermocline, and supports the productivity of both temperate and tropical upwellings in the South Atlantic and South Pacific (Toggweiler et al. 1991, Sarmiento et al. 2004).

In summary, the global pattern of marine primary and secondary productivity is well known, and is clearly based on nutrients that are eroded from the terrestrial land masses. These nutrients exert a direct effect on the productivity of the adjacent continental shelves and an indirect effect on other areas of the ocean through current transport and upwellings of nutrient rich water.

PATTERNS OF TERRESTRIAL NPP AND NUTRIENTS

The distribution of terrestrial NPP is generally presented in terms of the productivity of major ecosystem types, such as tropical wet forests, grasslands, boreal forests, etc. (Table 1). The first major effort to quantify terrestrial NPP was the International Biological Program (IBP) of the late 1960s and early 1970s (Leith and Whittaker 1975, Ajtay et al. 1979), and the accepted NPP values have changed little since then (cf. Saugier et al. 2001) (Table 1). Over the past decade or more, a number of physiologically based computer simulation models of NPP have been developed that use as input global climate data and satellite-based measurements of vegetation canopy density (leaf area index or a "greenness index"; Field et al. 1998, Cramer et al. 1999). The average results of these global vegetation models are consistent with earlier NPP estimates but provide more spatial detail (Kicklighter et al. 1999, see also Fig. 1B).

The most remarkable feature of the terrestrial NPP distribution is that it is the opposite of the pattern of marine NPP (Fig. 1B). Marine NPP is low near the equator and increases toward the poles, while terrestrial

TABLE 1. Historic (Ajtay et al. 1979, WBGU 1988) and current (Roy et al. 2001 [RSM]) estimates of total biomass (carbon density) and total net primary production (NPP; above- and belowground) in major biomes of the Earth.

Biome	Area (10^9 ha)		Carbon density (Mg C/ha)		NPP (g C·m^{-2}·yr^{-1})		Global NPP (Pg C/yr)	
	WBGU	RSM	WBGU	RSM	Ajtay	RSM	Ajtay	RSM
Tropical forests	1.76	1.75	120	194	783	1251	13.70	21.90
Temperate forests	1.04	1.04	57	134	625	779	6.50	8.10
Boreal forests	1.37	1.37	64	42	234	190	3.20	2.60
Tropical savannas and grasslands	2.25	2.76	29	29	641	540	17.70	14.90
Temperate grasslands and shrub lands	1.25	1.78	7	13	298	393	5.30	7.00
Deserts and semi-deserts	4.55	2.77	2	4	51	126	1.40	3.50
Tundra	0.95	0.56	6	4	179	89	1.00	0.50
Croplands	1.6	1.35	2	3	504	304	6.80	4.10
Wetlands	0.35		43		1229		4.30	
Total	15.12	14.93					59.90	62.60

Notes: WBGU is the German Advisory Council on Climate Change (1988), with forest data from Dixon et al. (1994). This table is based on Table 3.2 of IPCC (2001), which included values from Table 23-1 of Saugier et al. (2001) that had been converted from dry matter (DM) to carbon (C), assuming that 50% of dry matter is carbon. Values of NPP as g C·m^{-2}·yr^{-1} were derived by dividing global NPP by the global area of each biome (RMS area [10^9 g/ha^{-1}]).

NPP is greatest near the equator and decreases toward the poles. The current consensus is that tropical rain forest annual NPP is 60% higher than that of temperate forests (Kicklighter et al. 1999, IPCC 2001, Saugier et al. 2001; Table 1). How can we explain this paradox that terrestrial and marine productivity, both of which depend on mineral nutrients derived from the Earth's continents, have the opposite pattern with regard to latitude?

To answer this, we must first answer the question of why either terrestrial or marine productivity should be related to latitude in the first place. Why shouldn't productivity be related to geology? In fact, productivity is closely related to geological processes, which are the source of mineral elements from the Earth's interior, as well as the chemical processing and physical transport of these minerals that makes them available to organisms. However, there is no obvious latitudinal pattern of geological properties or processes (Huston 1993), other than climatically driven continental glaciation (Anderson et al. 2007). Volcanoes, which usually provide nutrient rich ash or lava that forms fertile soils, can be found at all latitudes along the Pacific Rim, as well as in Equatorial Africa. Geological processes such as volcanism, faulting, and mountain-building are not correlated with latitude.

Climate, on the other hand, clearly is related to latitude. The spatial pattern of the Earth's energy balance, and the global patterns of temperature and precipitation are well known to be the consequences of the angle of the Earth's rotational axis as it orbits around the sun, plus the inevitable change in the angle of incidence of solar radiation from direct (perpendicular to the Earth's surface between the Tropics of Cancer and Capricorn) to oblique (parallel to the surface near the poles). These geometric constraints on the input of solar energy to the Earth's surface, along with well-known processes of heat transfer through air and water, produce the distribution of heat (sensed as air and water temperature) and the resulting pattern of faster rates of evaporation of water vapor from warm water that makes precipitation much greater near the equator than near the poles. The various combinations of precipitation and temperature distributed over the Earth have a very predictable effect on vegetation type and structure (e.g., Holdridge 1947).

Temperature and precipitation affect NPP directly through their effect on the physiological processes of photosynthesis, respiration, and plant growth. The fact that photosynthetic rates increase asymptotically in response to increasing precipitation and have a temperature optimum with decreases to zero at very high and very low temperatures has been the basis of models of NPP for over 30 years (Leith 1975, VEMAP Members 1995, Ciais et al. 2001). Clearly, favorable temperatures for photosynthesis are found near the equator year-round, but are also found at high latitudes during the summers of the northern and southern hemispheres.

However, temperature and precipitation also have an indirect effect on NPP through their influence on the chemical and biological processes that form soil by dissolving and transforming the minerals found in the rocks that form the continental surfaces. The processes of mineral weathering occur much more rapidly under warm, wet conditions than under either cold or dry conditions (Brady and Weil 2002). This produces a characteristic pattern of soil depth and chemical properties in response to latitudinal patterns of temperature and precipitation (Fig. 3). Tropical soils tend to be deeply weathered, as well as acidic and low in available forms of most plant nutrients because of rapid weathering and nutrient loss through leaching (Sanchez 1976). In contrast, temperate and boreal soils tend to have much greater concentrations of essential nutrients because of lower rates of nutrient loss, greater organic matter content as a result of lower rates of organic matter decomposition (Meentemeyer 1978*a*, *b*, Post et al. 1982), and more frequent exposure and grinding of

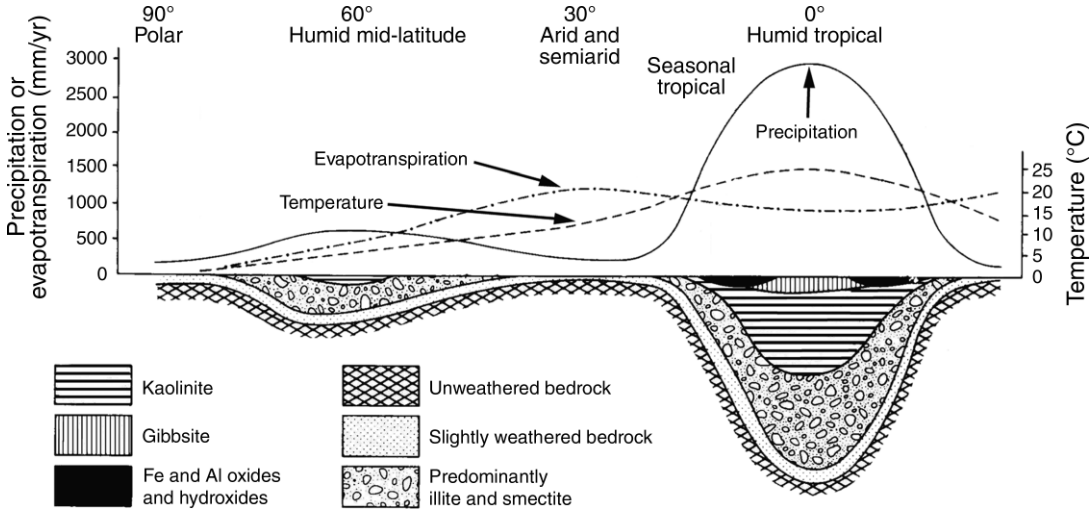

FIG. 3. Latitudinal gradient in soil structure and weathering depth in relation to climate and vegetation (based on Strakhov [1967]).

fresh minerals by the cycles of continental glaciation over the past 3 million years or longer (Van Andel 1994; Fig. 4A).

The basic processes of soil weathering have several inevitable consequences that result in a decline in soil fertility, and thus in the resources available to support plant growth and NPP over time as soils age. All of these processes occur most rapidly in the tropics. As phosphorus dissolves from fresh minerals, the phosphate anions (HPO_4^{-2} and $H_2PO_4^{-}$) bond with calcium cations and are readily available to plants. However, as soils age and C^{2+} and the other cations (K^+, Mg^{2+}, Na^+) are lost due to leaching and a reduction in cation exchange capacity (CEC) that occurs as clays weather (or organic matter declines), the phosphate anions bond with iron and aluminum oxides into very insoluble "fixed" forms that are essentially unavailable to plants (see Sanchez 1976:255–279, Brady and Weil 2002:592–620). Also as soils weather and age, the concentration of iron and aluminum increases as other cations are lost. Tropical oxisols and ultisols sometimes have such a high concentration of these metals that the soils and their concretions are mined as ore. One consequence of these high iron and aluminum concentrations is that most of the phosphorus in these weathered soils, which may be a relatively large total amount of P, is almost completely unavailable to plants. Plant symbioses with mycorrhizal fungi can increase the ability of plants to get at least some phosphorus where P concentrations are extremely low (e.g., Lambers et al. 2008).

A second major consequence of soil weathering is a gradual decline in pH (i.e., increasing acidity) over time. This occurs because the mobile nutrient cations (Ca^{2+}, K^+, Mg^{2+}, Na^+), which are retained in the soil by negative charges on clay surfaces and organic matter, are lost by leaching, leaving the hydrogen ion (H^+), as well as immobile iron and aluminum compounds and their associated cations as the dominant cations. High concentrations of H^+ reduce pH. Consequently, most old or highly weathered soils, such as tropical Oxisols and Ultisols, are very acidic. Soil pH is strongly correlated with soil cation exchange capacity and total exchangeable bases (see Huston 1993), so a global map of soil pH would show the same basic patterns seen in Fig. 4A. In addition to potentially leading to aluminum toxicity, low pH further reduces the availability of whatever phosphorus is in the soil. Phosphate solubility is highest around a pH of 6 to 7 and declines to low levels below a pH of 5. Most tropical oxisols and ultisols have a pH between 4 and 5, and thus extremely low phosphorus availability (Uehara and Gillman 1981, Brady and Weil 2002:610), as well as very low availability of the base cations (Ca^{2+}, K^+, Mg^{2+}, and Na^+; Fig. 4A).

Nitrogen is another part of the soil fertility story. Because the primary source of nitrogen is the atmosphere, there is no inherent latitudinal pattern of nitrogen availability. However, nitrogen fixation requires energy from plants, so there is potentially greater N fixation where plants have large amounts of all the other soil nutrients they need to grow well, except for nitrogen, which legumes and a few other types of plants can get from their microbial, algal, or fungal symbionts. Consequently, there tends to be more nitrogen accumulation in soils with higher phosphorus availability (e.g., Walker and Adams 1958), and thus more nitrogen in many temperate soils compared to the nutrient-poor oxisols and ultisols that underlie most rain forests (Post et al. 1985). The largest difference between tropical and temperate soils is not, however, in their nitrogen availability, but in their phosphorus availability, which is much lower in the tropics. Consequently, the ratio of nitrogen to phosphorus (N:P) tends to be higher in tropical soils (Zinke et al. 1984) and in the leaves of tropical trees (Vitousek 1984) because phospho-

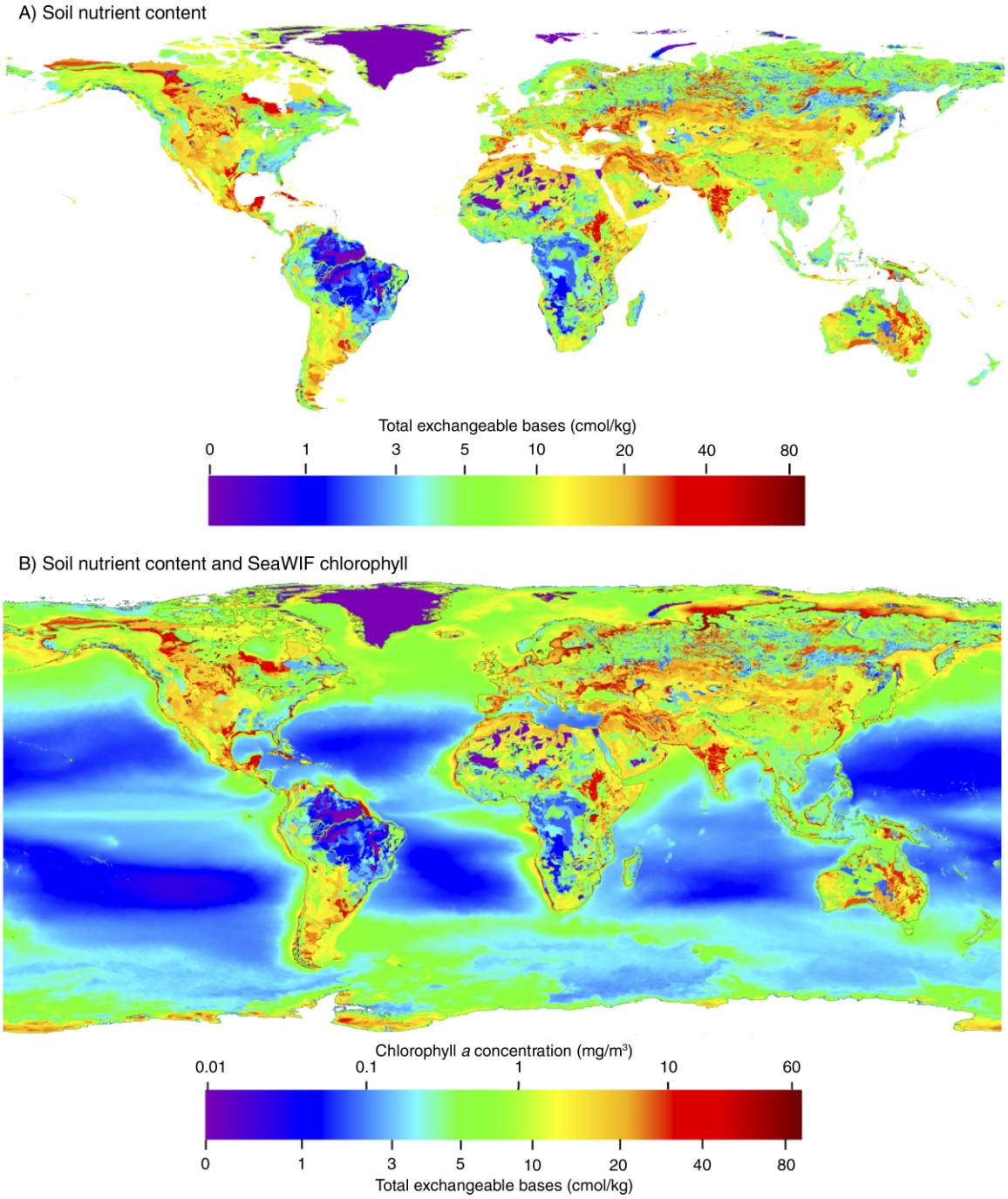

FIG. 4. Global distribution of soil fertility and marine chlorophyll concentration. (A) Soil fertility, as estimated by total exchangeable bases (K, Ca, Mg, Na) in the FAO Soil Map of the World (Food and Agriculture Organization of the United Nations 2008). (B) Terrestrial total exchangeable bases superimposed on ocean chlorophyll for reference.

rus availability is so low. These patterns have led to the generalization that tropical systems tend to be limited by phosphorus, while temperate systems tend to be limited by nitrogen, both for NPP and potentially for decomposition of dead plant material (Aber and Melillo 1980, Melillo et al. 1982, Walbridge and Vitousek 1987, Vitousek and Howarth 1991, Cleveland and Townsend 2006).

However, the concept of "limiting nutrients" can be misleading in the context of regulating NPP. Plants require a variety of mineral nutrients in relatively specific proportions, e.g., "macronutrients" and "micronutrients," analogous to the "Redfield Ratio" of 106 C:16 N:1 P in marine phytoplankton (Redfield 1958, Redfield et al. 1963). Addition of more of the limiting nutrient will only

increase NPP up to the level allowed by the availability of the next most limiting nutrient. In many tropical soils, where the availability of most essential plant nutrients is low, adding more of the currently limiting nutrient may not result in much increase in NPP. Nonetheless, the physical properties of tropical ultisols and oxisols are quite good, so if their deficiencies of micro and macro nutrients are eliminated by appropriate fertilization, they can become much more productive (Sanchez 1976, Uehara and Gillman 1981).

Thus, the nutrient deficiencies of tropical soils are an inevitable consequence of the higher rates of nutrient loss and immobilization under warm wet conditions, as well as their age. Ancient soils in most parts of the world have lower nutrient availability than younger soils, and we would expect this general pattern to have existed over most of the history of terrestrial life on earth. It is a coincidence of geological history that two of the major tropical forest regions, in Africa and South America, are located on ancient level plains with little recent tectonic or glacial activity to provide fresh parent material for soil formation. The third major tropical forest region, the Malay Archipelago, has much more recent mountain-building activity, and more fertile soils than the other two regions (Richter and Babbar 1991) (Figs. 4A and 5). Outside the tropics, extremely nutrient-poor soils are found on ancient landscapes, some of which may have experienced more tropical conditions in the past, such as much of Western Australia (McArthur 1991, McKenzie et al. 2004).

In spite of local variability due to volcanism, mountain building, erosion, and deposition, the global pattern of soil fertility has a clear latitudinal gradient from predominantly low-nutrient soils in the tropics, to predominantly high-nutrient soils in the mid and upper latitudes (Fig. 4A). This global distribution of total exchangeable bases, as well as of other aspects of soil fertility, closely parallels the pattern of marine productivity (Fig. 4B), which is based on terrestrially derived nutrients. It is not a coincidence that the most intensively cultivated soils on the planet are the fertile soils of the temperate zone, particularly in the northern hemisphere, and not the infertile soils of the lowland tropics (Huston 1993, 2005).

Addressing the Paradox

The fundamental question we must answer to explain or resolve this paradox of opposing marine and terrestrial NPP gradients is: Why should marine productivity be positively correlated with the availability of mineral nutrients in the oceans and the adjacent continents, while the productivity of the plants growing in the soil on those continents is inversely correlated with nutrient availability?

There are several ways in which marine plants and their NPP differ from terrestrial plants and their NPP. The primary difference is in the total plant biomass per unit area found in the two systems. Total biomass per unit area or volume in marine systems, particularly of the phytoplankton responsible for most marine NPP, is much lower than the total biomass of terrestrial systems, where the woody structure of trees can reach 20 kg or more of dry mass per square meter of land surface (Cannell 1982, Olson et al. 1983, Brown and Lugo 1984, 1992, Brown et al. 1993, 1995, Brown 1997, 2002). In contrast, phytoplankton can reach 1 or 2 g/m^3 (Irigoien et al. 2004) and kelp (*Macrocystis pyrifera*) up to 1.66 kg dry mass per m^2 in patches (Rassweiler et al. 2008).

Another way to evaluate this difference is through the ratio of photosynthetic tissue to supporting tissue, which respires carbon fixed by photosynthesis, but does not perform photosynthesis. The large amounts of these tissues in the boles, branches, and roots of terrestrial plants are critical for providing support to elevate the leaves into the sunlight, as well as for roots to obtain nutrients and water from the soil to sustain the leaves in the plant canopy. In terrestrial plants the mass ratio of supporting (and respiring) tissues to photosynthetic tissues ranges from 1:10 in annual herbaceous plants (Parsons 1967) to 100:1 or higher in large trees (Cannell 1982). This is one reason that it is easier to estimate NPP in marine plants than in terrestrial plants. In marine plants virtually all the plant tissue is directly involved in photosynthesis, so its mass provides a direct estimate of current NPP. In contrast, in terrestrial plants, most of the plant tissue is not involved in photosynthesis, and in fact is actually respiring photosynthate, and thus its respiration must be subtracted from leaf net photosynthesis to determine NPP. This is one reason that the amount of chlorophyll (or leaf area, which can be estimated from satellites) in terrestrial plants does not provide a good estimate of terrestrial NPP, because the total respiration of all non-photosynthetic tissue, the mass of which is very difficult to determine, must be subtracted from the gross photosynthesis of the leaves.

Yet another difference is in the surface to volume ratio of the photosynthetic tissues, which is vastly higher in phytoplankton, as well as the much greater dissolved nutrient content of water compared to air. Phytoplankton can usually obtain all the nutrients they need from the watery medium in which they grow, while tree leaves depend on belowground roots and an elaborate vascular system to deliver the water and nutrients they need. In terrestrial plants, the biomass ratio of belowground root systems to aboveground tissues (stems, trunks, branches, and leaves) ranges from 10:1 in some grassland plants to 1:10 in certain forests (IPCC 2003: Table 3A.1.8).

All of these differences suggest that the relative efficiency of NPP (mass of carbon converted to plant tissue per photon of light received) should be higher in marine/aquatic systems than in terrestrial systems. Thus, there are no obvious reasons that terrestrial plants should have greater NPP where nutrient availability is low while marine/aquatic plants should have greater productivity where nutrient availability is high. If anything, it seems as if marine/aquatic plants should

grow relatively better where nutrient availability is lower, because of their greater efficiency of nutrient uptake and their reduced burden of supporting tissues. Further questions are raised by the fact that there is a strong terrestrial latitudinal gradient of agricultural productivity, as revealed by a variety of measures, from low productivity in the tropics to high productivity in the high latitudes (Huston 1993, 1994, 2005, Green et al. 2005: Fig. 1C). Why should the productivity of natural ecosystems have a latitudinal pattern that is the opposite of the productivity of agro-ecosystems?

With no convincing mechanisms to resolve this paradox, we must consider the possibility that one of the accepted patterns is wrong. The data on marine productivity, both satellite-based chlorophyll measurements, and the history of marine fisheries and whaling, leave little doubt about the marine pattern of NPP. However, there is substantial direct and indirect evidence to suggest that it is the presumed latitudinal gradient of terrestrial NPP that is in error. This evidence, including both direct measurements of NPP and a number of plant and animal properties that could be expected to be correlated with NPP, will be presented in the following sections and some of the implications of a revised understanding of global NPP patterns for ecological and evolutionary theory will be addressed in the discussion.

Direct Measurements of NPP in Forest Ecosystems

Understanding the global pattern of forest productivity and biomass is complicated by the heavy impact of human activities on most of the Earth's forests. Throughout the world, the forests on the most productive soils have been cleared and the land converted to cultivated agriculture (Whitney 1995, Russell 1997, Laurance et al. 2001, Huston 2005). In North America, Europe, and throughout much of the tropics, the forests on the best soils were cleared long before there was any scientific or economic incentive to quantify the structure of the forests. Only in the humid tropics, and a few scattered areas in the rest of the world, have mature forests survived the 20th century with minimal human impact.

As a consequence of this historic sequence of forest clearing, most of the scientific measurements from tropical rain forests represent mature, relatively unimpacted forests, while most of the measurements from the temperate zone are from forests that have been impacted by removal of the largest and most valuable trees over the past several centuries, or are from forests that have re-grown following earlier clearing or logging. The remaining undisturbed forests outside the tropics have survived primarily because they are located on infertile and unproductive soils and were not sufficiently valuable to harvest or convert to agriculture.

With the caveat that temperate forests have generally been more degraded by human activities than tropical forests, at least until recently, there are sufficient data on

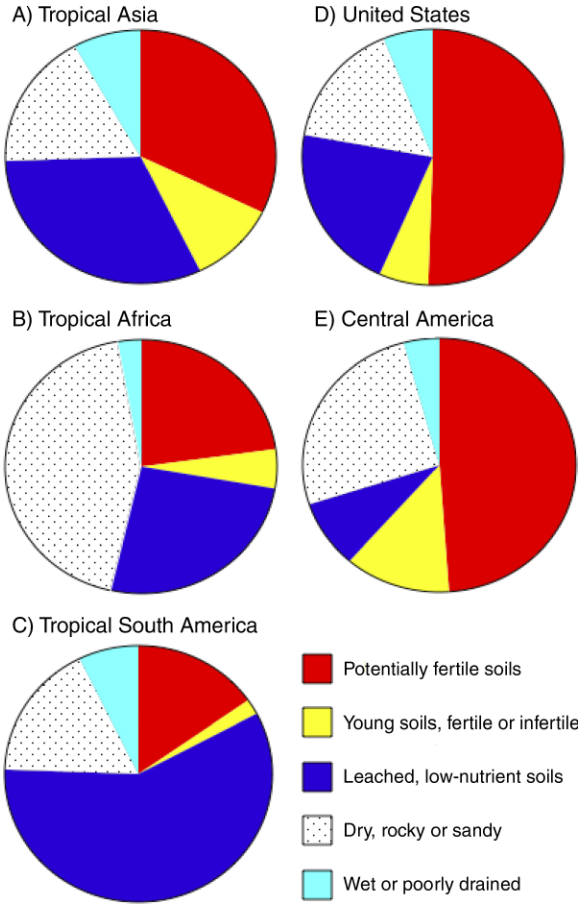

FIG. 5. Relative distribution of soil types with differing fertility properties among the three major tropical regions of the world, with the United States and Central America for comparison. Values for Asia, Africa, and South America include only the area between 23°30′ N and 23°30′ S (based on Richter and Babbar 1991). Note that tropical South America has the lowest proportion of potentially fertile soils and the highest proportion of leached, low-nutrient soils of the major tropical forest regions.

a number of forest properties from sites scattered (unfortunately unevenly) across the globe (e.g., Cannell 1982), that it is possible to draw some preliminary conclusions about global patterns of forest structure and productivity in mature forests. It is well known that young, early successional forests have higher rates of NPP than mature forests (O'Neill and DeAngelis 1981, Pregitzer and Euskirchen 2004), primarily because of their higher ratio of photosynthetic tissue to supporting tissue, so it is important that comparative data be based on forests of similar age, specifically those considered to be "mature" forests.

Conceptually, NPP is simply the total amount of carbon that a plant converts to sugar and its derivatives through photosynthesis and subsequent processes (called gross primary production or GPP), minus the amount of that carbon that is respired by the plant. NPP is typically reported, and usually measured, as an annual

rate. In practice, NPP has many components, some of which are very difficult to quantify, and are thus rarely measured (Clark et al. 2001*a*, *b*). The two largest components of NPP are the production of wood, which is a long-lived tissue, and the production of leaves, flowers, and other short-lived tissues. The aboveground production of wood and short-lived tissues is relatively easy to measure and comprises the vast majority of available NPP data. However, belowground production of woody roots and short-lived fine roots can form a significant proportion of total production (Vogt et al. 1986, 1996, 1998, Raich and Nadelhoffer 1989, Jackson et al. 1996, 1997, Cairns et al. 1997, Nadelhoffer et al. 1998, Clark et al. 2001*a*, *b*) but is extremely difficult to quantify. Consequently, the most reliable component of NPP data is the aboveground component, and the belowground component is usually estimated with substantial uncertainty. Since most vegetation models used in global change and carbon cycle research estimate total NPP, including both above- and belowground production (Cramer et al. 1999), the accuracy of the model predictions is difficult to test precisely.

The historical NPP data vary in quality and methodology. A recent effort to compile and evaluate these data identified a total of 81 high-quality measurements (class A data) with supporting environmental data, many of which come from a few locations (Scurlock et al. 1999, Olson et al. 2001*b*, Scurlock and Olson 2002). Of the approximately 40 sites classified as forest (Fig. 6A), there is obviously no significant difference between the mean values for aboveground NPP in tropical vs. extratropical sites (Fig. 6D).

When more sites, including many with less complete documentation than the class A sites, are considered, the basic pattern remains the same (Fig. 6B). Sites with a broad range of NPP are found both within and outside the tropics, and the latitudinal pattern shows somewhat larger values in the temperate zone as compared to the tropics, plus a clear decline at the highest latitudes (Fig. 6E). An even bigger data set, with more boreal, Australian, and Chinese sites (Fig. 6C) shows the expected decline in NPP at polar latitudes where the growing season is very short (Fig. 6F), but also includes some large tropical values from regions not included in the previous two data sets.

In the larger data sets, spatial patterns can be resolved that are independent of latitude. High values appear to be concentrated in areas with more geological activity, such as around the Pacific Rim and in the Indo-Pacific (Fig. 6B, C), both of which have relatively fertile soils (Figs. 4A and 5). The limited number of tropical sites suggests that ANPP may be lower in the Neotropics than in Africa or Southeast Asia, which would be consistent with the differences in soil properties among these regions (Figs. 4 and 5, see also Richter and Babbar 1991). These geographical variations have a strong influence on patterns in data sets with differing geographical distributions of sample sites, particularly when the total number of samples in a latitudinal band is small (compare Fig. 6E, F). Sites in New Zealand and southeastern Australia (Fig. 6B) appear to have much higher NPP than other sites at the same latitude (Fig. 6C). New Zealand's North Island has active volcanoes, and southeastern Australia has had volcanic activity as recently as 9 million years ago.

These results, which on average show no difference in annual NPP between temperate and tropical forests are in direct conflict with the global pattern of NPP taught in ecology textbooks and found in the latest modeling results (Fig. 1B; Field et al. 1998, Cramer et al. 1999, Kicklighter et al. 1999, Potter 1999) and IPCC reports (IPCC 2001), which state that tropical rain forests are the most productive terrestrial ecosystems on the planet, and that the average annual NPP of tropical rain forests is approximately 60% greater than that of temperate forests (Kicklighter et al. 1999, IPCC 2001, Saugier et al. 2001) or as much as 170% greater (Potter 1999). Could there be some undetected bias present in the physical measurements of forest NPP that might skew the results? This seems unlikely, but it is worth looking at different types of information to evaluate whether the directly measured NPP values are consistent with other data related to forest productivity, such as wood density and relative allocation to wood vs. leaves, as discussed in the following sections.

While forests are particularly important for wood products and biodiversity, it is clearly important to understand the NPP of other ecosystem types as well. There is a general consensus, with no contradictory information, that most wetlands, tropical or temperate, tend to be extremely productive (Table 1), although there is undoubtedly variation in monthly NPP as a result of differences in substrate nutrient content, and in annual NPP as a result of growing season length. Of vegetation types with low productivity, tundra has a very short, temperature-limited growing season, which obviously limits annual NPP, and deserts have a short, water-limited growing season and are chronically limited by low water availability.

Grasslands and savannas are two additional ecosystem types that are extremely important to biodiversity, particularly of large animals and grassland specialists. The high productivity of grasslands and the fertility of grassland soils are well known (Table 1), and for this reason, most of the world's productive grasslands have been destroyed by cultivation (Huston 2005). Rainfall is considered to be the primary driver of differences in grassland productivity (e.g., Walter 1973: Fig. 129, 2002), while a combination of temperature and lack of precipitation determines the length of the growing season and thus annual NPP. Grasslands occur where rainfall is insufficient to support forests, but grassland soils are typically high in mineral nutrients and organic matter, and are consequently very productive when there is adequate precipitation. Unfortunately, the

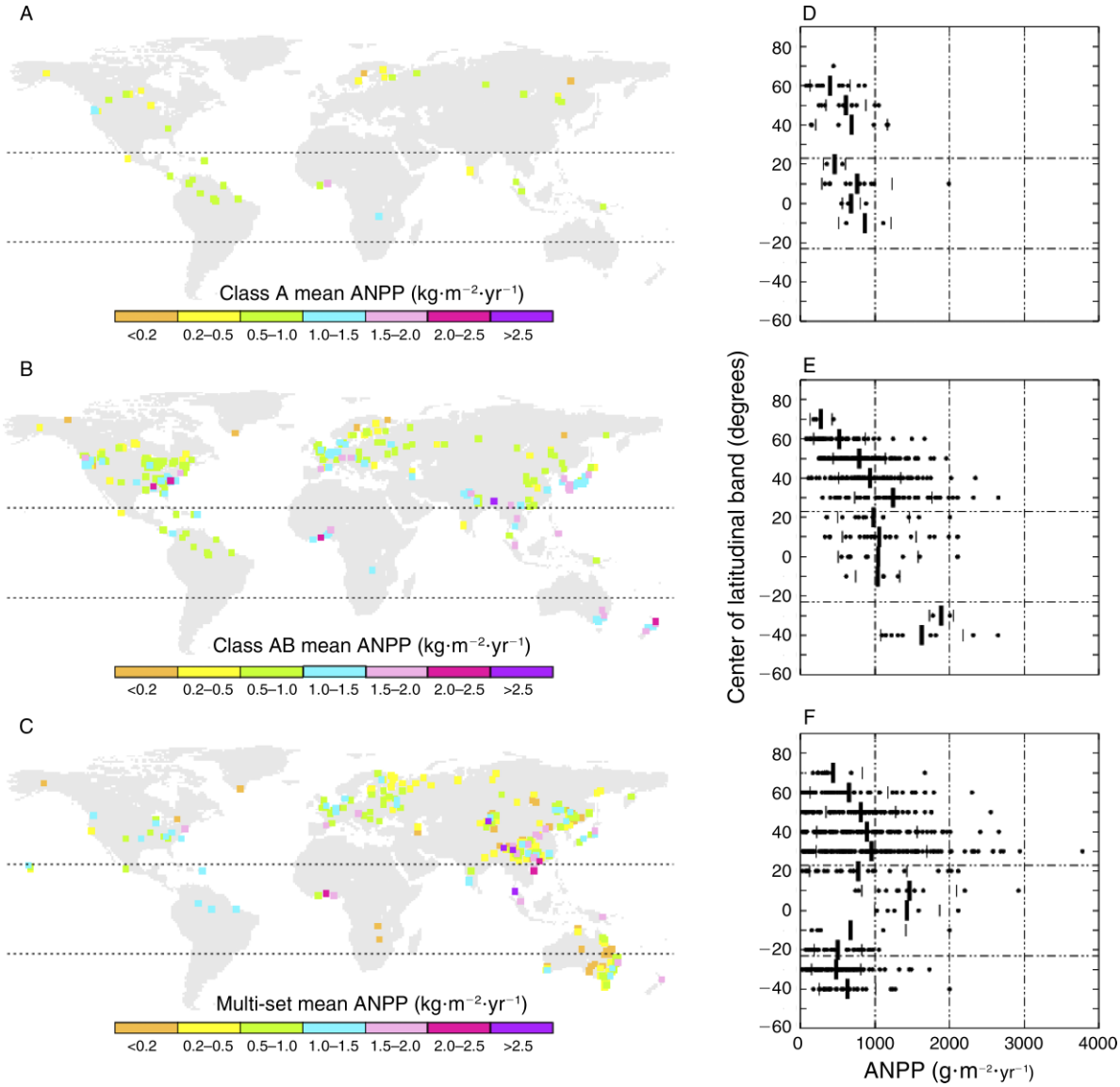

FIG. 6. Global distribution of annual aboveground NPP estimates (ANPP) for forests around the world (minimum age of 100 years, where age is given, otherwise "mature") for three compilations of data: (A) 40 class A (extensive documentation and ancillary data) sites from Olson et al. (2001*b*); (B) 362 class A and B (less extensive documentation and ancillary data) sites from Olson et al. (2001*b*); and (C) 755 sites from a compilation of six historical data sets (variable documentation and quality assurance) (DeAngelis et al. 1997, Esser 1998, Barrett 2001, Clark et al. 2001*b*, Denissenko et al. 2001, Ni et al. 2001). Each colored square (3° × 3°) represents the mean of all data values within a 0.5° × 0.5° area centered on the square. The number of data values is 1 for most cells, but as high as 20 for some. Highest ANPP values are placed "on top" of lower values where overlap occurs. Panels D–F show latitudinal patterns of annual ANPP aggregated by 10° bands (all data are shown with mean [thick vertical bar] ± SD [thin vertical bars]; negative values are south of the equator) for the three compilations of data in panels A–C, respectively.

global data on grassland productivity are extremely limited, and plagued with methodological inconsistencies (Scurlock et al. 2002) that make it impossible to confirm global patterns.

Because forests of all types are more widely distributed and cover more area (4.17×10^9 ha, Table 1) than any other single nondesert vegetation type (3.5×10^9 ha for grasslands and savannas, Table 1), and because much more data have been collected from forests, at least partially because of their economic value, forests provide the best globally distributed data for evaluating patterns of NPP. The following sections address several additional types of data for forests and trees, all of which are consistent with the forest NPP data presented above, and thus inconsistent with the accepted beliefs about the global pattern of NPP.

Tree Size and Forest Mass

The measurements of forest NPP discussed above involve a number of assumptions, as well as estimates that are potentially subject to considerable error (Clark et al. 2001*a*, *b*, Clark 2002, 2004). A critical step is estimating the annual change in the mass of the wood in the trunk and branches of an entire tree from the annual change in its diameter at one position 1.37 m above ground level. While there is considerable uncertainty in this estimate of annual change in biomass (a small number obtained by subtracting one large number from a slightly larger number), there is much less uncertainty in the estimation of the total woody mass of an individual tree, which is a single large number.

The size and number of trees in a forest is an important economic indicator in forest management, as well as an indication of both the total amount of biomass (and thus carbon) in that area, and of the physical structure available to support other plants and animals. This information is often summarized as total biomass, which can be estimated fairly accurately with labor-intensive methods (Brown and Lugo 1984, 1992, Brown et al. 1993, 1995, Brown 1997, 2002, Gaston et al. 1998, Houghton et al. 2001). Standard methods estimate forest biomass by summing estimates for individual trees that are based on regressions on tree diameter. While tree diameters are easily measured, the required biomass regression parameters are difficult to estimate and vary from one forest to another and from one tree species to another (Tritton and Hornbeck 1982, Ter-Mikaelian and Korzukhin 1997, Araujo et al. 1999, Clark et al. 2001*b*). The tree diameter data from an area of forest can also be simply summarized as total basal area (m^2/ha or square feet per acre), which provides a metric that is consistent and free from estimation errors.

Total basal area and maximum tree height are commonly used indicators of forest mass and productivity for forest management. The quantification of "site index," used by foresters to compare tree growth rate (and thus potential economic return) on different parcels of land, is based on the height of trees after a specific period of growth (e.g., 20 or 30 years). The greater the height or basal area that a stand of trees reaches within a specified period of time, the greater the productivity of the stand in terms of either harvestable timber or total biomass. Since trees continue to increase in diameter and height as they grow, the relative basal area of forests of the same age and stem density provides an indication of their relative long-term productivity (as well as of their relative biomass at that age). Measuring the biomass of multiple forests of the same age would provide a correlate of their NPP, minus the amount that is shed as dead leaves and wood each year, and subsequently decomposed.

Quantifying the actual amount and distribution of forest basal area (and regression-based biomass estimates) over the globe, as might be needed for "carbon accounting," would require systematic stratified random sampling and measurement of all existing forests, ranging from degraded or successional forests to undisturbed, old-growth forests (Brown and Gaston 1995, Brown 1997). Even if this were feasible, the difficulty of estimating the age of forests would make it impossible to use this information to estimate NPP. However, determination of the maximum potential forest basal area in any region, which is presumed to be equivalent to the maximum basal area prior to major human impacts, requires measurement of only the mature forests that have been minimally affected by human activities (but which are still affected by natural sources of mortality). This information should provide a correlate of forest NPP, and, in general, estimates of mean biomass for the major forest types of the world are strongly correlated with NPP (O'Neill and DeAngelis 1981, however, see Keeling and Phillips 2007). Recent summaries of the properties of global vegetation types, which generally include both NPP and total biomass, report that tropical forest biomass is 45% (Saugier et al. 2001), 87% (Houghton and Skole 1990, Potter 1999), or 110% (WBGU 1988) greater than the biomass of temperate forests.

A compilation of published basal areas of mature and "old-growth" forests from over 900 measurement plots (Cannell [1982] and other sources listed in Supplement 1) indicates that mean basal area in tropical forests is only about 70% of that in the temperate latitudinal bands with the highest basal areas (Fig. 7B), and that most of the sites with the very high basal area are outside of the lowland tropics (Fig. 7A). There is a general pattern of large basal areas around the Pacific Rim and other areas with volcanism or mountain building, large values in the temperate latitudes of North America, Europe, and Eastern Asia, and consistently low basal areas in the tropics of the Western Hemisphere, and Africa (Fig. 7A). The tropical forests of the Indo-Pacific region have the largest basal areas of the three tropical regions, which is consistent with the more fertile soils of this region (Figs. 4A and 5) and with reports that these forests also have the greatest tree heights (Whitmore 1984). Patterns of global wind speed suggest that part of the explanation for the unusual structure of these forests may be the fact that average surface wind speeds in the region are among the lowest on the globe (Lagerloef et al. 1999).

The conspicuous distribution of high basal areas around the Pacific Rim and in other geologically active areas suggests that greater soil fertility, resulting from more frequent tectonic activities that produce or expose fresh minerals, is a primary cause of the high forest biomass (and probably also NPP) in these areas. This pattern is seen in both tropical and temperate climate regions, and provides the primary exception to generalizations about the low fertility of tropical soils (Fig. 4A; Huston 1993, 1994). In addition to areas with recent tectonic or volcanic activity, high basal area also tends to occur in riparian and alluvial areas, where nutrient-rich sediments derived from geologically active moun-

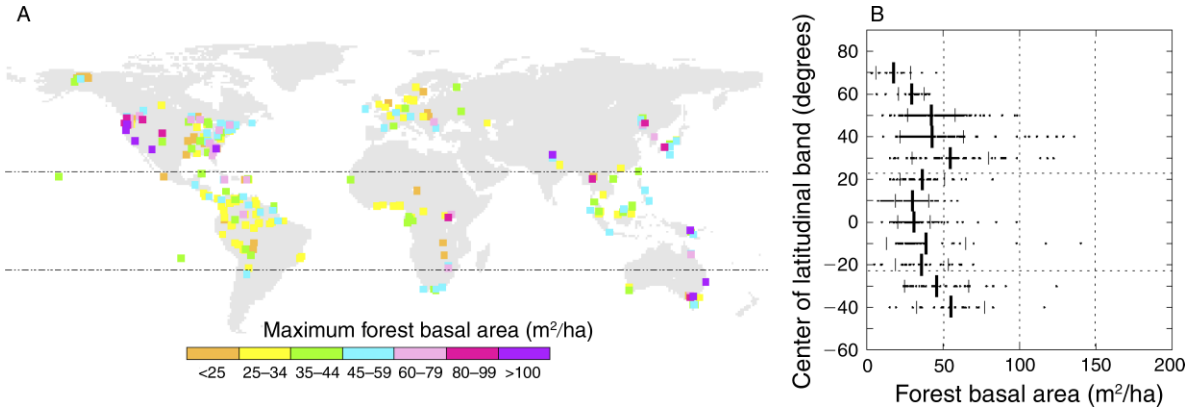

FIG. 7. (A) Maximum basal areas measured in over 800 mature forest sites around the world (minimum age of 50 years). Note that the colored squares cover a 3° × 3° area centered on the 0.5° × 0.5° cell where the data were collected. (B) All data from panel (A) by 10° latitudinal bands, showing mean ± SD as described in Fig. 6. References for all sites from Cannell (1982) and other sources are listed in Supplement 1.

tains accumulate, as well as in lowland areas with Pleistocene glacial activity.

The data on forest basal area described above convincingly demonstrate that tropical forests do not have the largest trees and probably not the greatest biomass of all forest types. Forest basal area appears to be strongly correlated with soil fertility, with great variability due to both latitudinal and longitudinal variation in climate and geology. However, total basal area data are problematic for estimating tree growth rates or NPP because of uncertainty whether all measured forests are even roughly the same age. Nor does basal area correlate directly with total forest biomass, because forests of the same basal area can differ in tree height and also because trees with different growth rates can vary significantly in wood density (see *Global variation in wood density*).

Global Variation in Wood Density

Wood properties are relevant to the global carbon cycle and to ecological processes because they affect the resistance of trees to damage, they affect the rate at which dead wood decomposes, and they provide an indication of how rapidly the wood was produced. Although wood properties are not typically measured in ecological research, the wood products industry has collected a large amount of information about the wood of tree species, including density (Bolza and Kloot 1963, Llach Cordero 1969, Chudnoff 1979, Alden 1995, 1997).

Wood density provides important information about the growth rate of trees, and, by inference, the productivity of the forests in which they grew. Foresters have long recognized that fast-growing trees produce lower density wood than more slowly growing trees in both interspecific and intraspecific comparisons (Mitchell 1965, Walgren 1965, Yanchuck et al. 1983). Extreme contrasts include the well known low density wood of the extremely fast-growing balsa tree (*Ochroma* sp., density 0.13–0.16 g/cm^3), vs. the dense wood of slowly growing trees such as lignum vitae (*Guaiacum* sp., density 1.05).

Determining mean wood density of a forest is more difficult in the tropics, where the number of tree species in most forests is very large (Fearnside 1997), than in the temperate zone, where most forests are dominated by one or a few species. Mean volume-weighted density values for Brazilian forests confirm that these forests have higher wood density than most temperate forests (Fig. 8A–E).

Mean wood density values collected by the wood products industry for tree species that are found in various parts of the world reveal several clear patterns: (1) the very productive coniferous forests of the Pacific Northwest of North America are composed predominantly of species with low-density wood, as are the forests of the western intermontane region (Fig. 8A, B); (2) the proportion of species with low-density woods increases with latitude in eastern North America (Fig. 8C–E); (3) Australian tree species, both tropical and temperate, have much greater wood densities than species found at equivalent latitudes in the New World (Fig. 8A vs. F, and 8G vs. J); and (4) the major tropical rain forest regions have differing distributions of wood densities, with species of tropical Asia having the narrowest range of densities, and lowest median density, and tropical America having the widest range, and the greatest median density (Fig. 8H–J; see Plate 1).

There is no doubt that the tree species with the densest woods are found in the tropics, although the tropics (particularly South America) also include the lowest density woods (Fig. 8J). This contrast has two major implications: (1) for forests with the same wood volume, tropical forests are likely to have biomass that is greater by 15–100% than temperate forests (note that these differences are accounted for in species or region-specific regressions for estimating biomass from diameter, e.g., Brown 1997); (2) tropical trees grow more slowly than most temperate trees, implying that the rate of wood

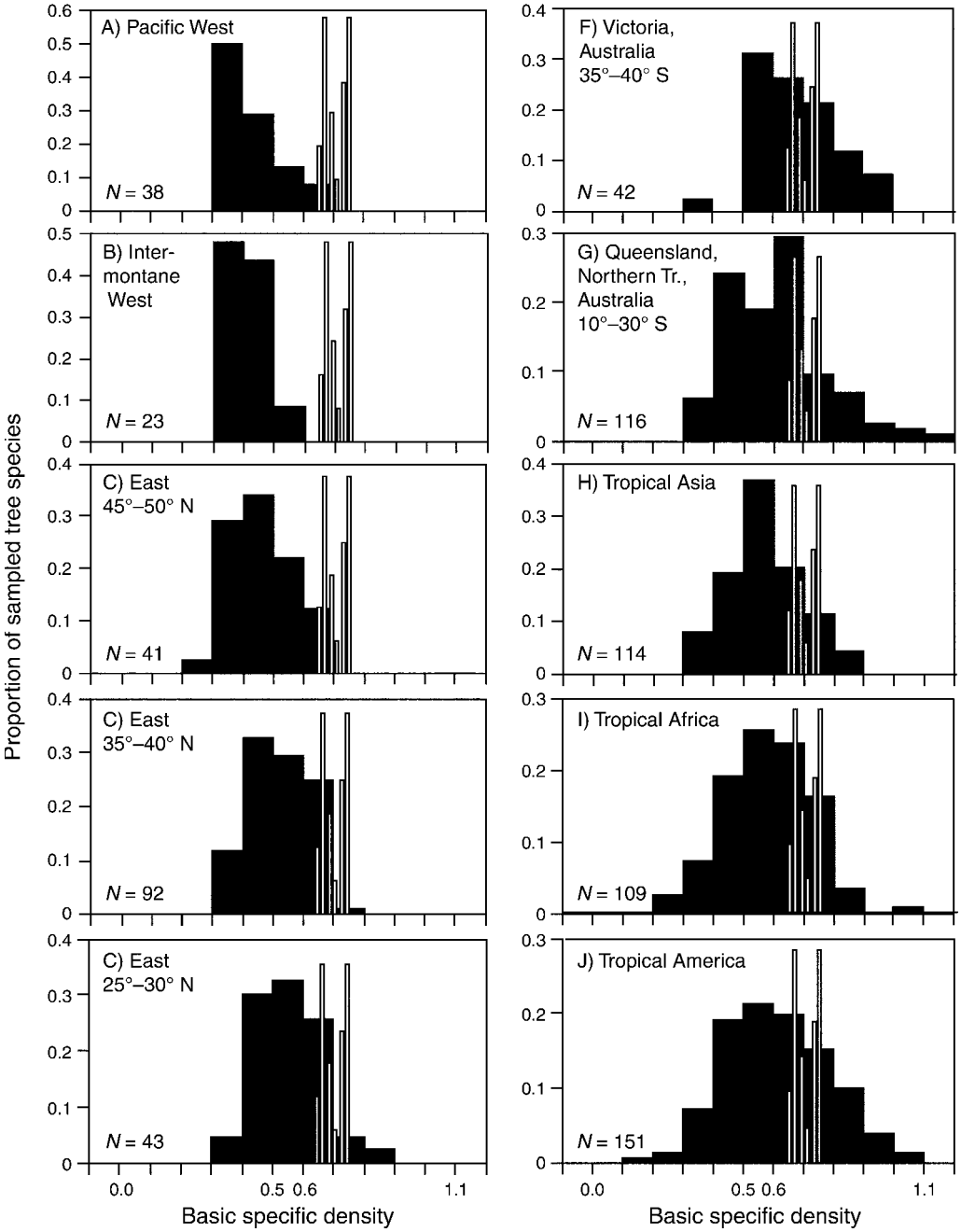

FIG. 8. Wood densities of tree species found in different regions. Histogram height indicates the proportion of all tree species for which data were available (total number indicated by *N* in the lower left) in density classes of 0.1. Panels A–E are for species found in subregions of North America; panels F–J are Australian and tropical species. Open thin bars show volume-weighted values for total forest wood density for 45 sites in Amazonian "dense forest," with the density of each species (where known) weighted by the volume of that species in the forest (Fearnside 1997). Basic specific density is calculated as the oven-dry mass of a sample of wood, divided by the volume of that wood when freshly cut (green volume) in units of g/cm^3 (based on data from Bolza and Kloot [1963], Chudnoff [1979], and Alden [1995, 1997]).

production during the growing season is actually greater in the temperate zone than in the tropics.

As expected, the broad patterns of wood density are inversely related to the patterns of forest NPP described previously. While the largest NPP values are found in areas of rich soils in both temperate and tropical regions, the highest density woods are associated with areas of poor soils, and sometimes also aridity (Chave et al. 2006), in both tropical and temperate regions. The ancient and nutrient-poor soils of most of temperate

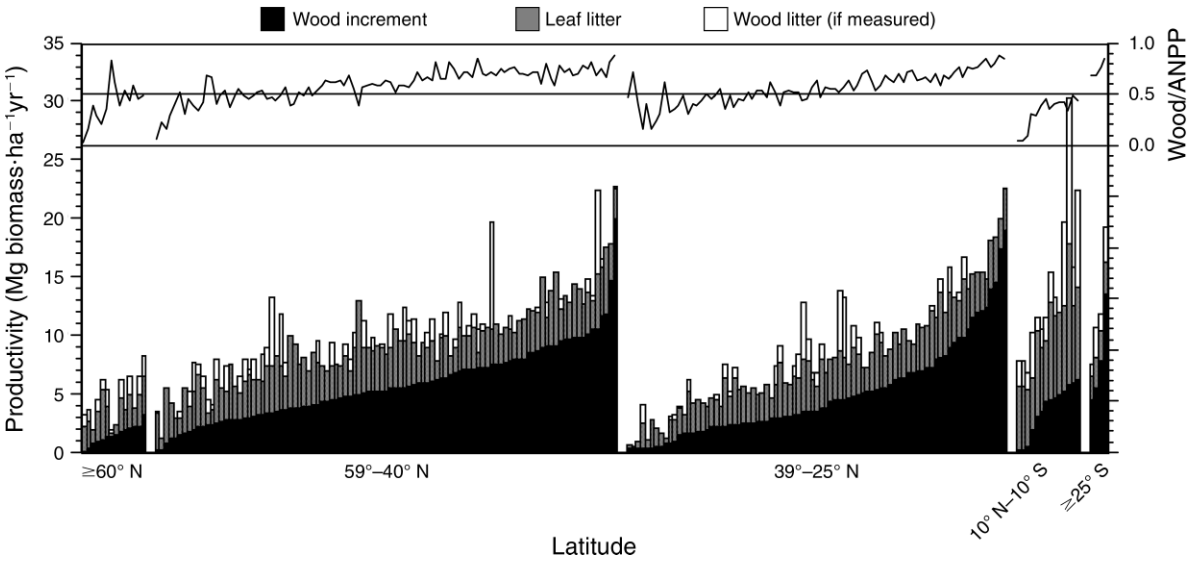

FIG. 9. Major components of aboveground NPP in forests by latitudinal bands from north to south. All studies measured leaf litterfall and estimated biomass increase based on diameter measurements. Relatively few studies measured litterfall of dead wood (twigs, branches, and fallen trees). The upper line graph indicates the proportion of ANPP (defined as leaf litterfall plus wood production) that is contributed by wood production. Sites correspond to references listed in Supplement 2.

Australia (McArthur 1991, McKenzie et al. 2004) contrast with the fertile, recently glaciated soils of equivalent latitudes in North America and Europe, and are consistent with the very dense woods of Australian tree species. Likewise, in the tropics, the contrast between the higher wood densities of South American tree species in comparison with those of Asia is consistent with the fact that South America has the largest relative (and absolute) area of infertile soils of the three major rain forest regions, while Asia has the largest relative areas of fertile soils (Figs. 4 and 5). Even within Amazonia, wood density is greater on the poor soils of the central and eastern regions and lower in western Amazonia closer to the Andes where the soils are better (Baker et al. 2004, Chave et al. 2006) (see Fig. 4A). Wood density of tree species found in dry forests in Central and South America, where tree growth is slowed by lack of water, have even denser wood than rain forest species (Chave et al. 2006).

There are many reasons why a tree might be growing slowly in terms of diameter increase and wood density. The same amount of lignin and cellulose could potentially be used to make either a thick growth ring of low-density wood, or a narrow growth ring of greater density. This is clearly an issue of the carbon allocation and life history strategy of the plant, in relation to height growth, wood strength, longevity, and potentially other uses of carbon for chemical defense, root growth, support of mycorrhizal fungi, etc. (e.g., Loehle 1988). Unfortunately, belowground carbon allocation is very difficult to measure (Clark et al. 2001*a*, *b*), so the information needed to fully understand the effects of belowground carbon allocation on aboveground stem growth is not available. However, there is a great deal of information on the relative allocation of NPP to leaves vs. wood. Leaf growth is often assumed to be proportional to root growth, because roots provide both the mineral nutrients and the water required by the leaves.

Global Variation in the Ratio of Wood to Leaf Production

The two primary components of aboveground NPP, wood and leaf production, have very different implications for the global carbon cycle, as well as for ecological processes. Leaves, flowers, and fruit are generally shed by trees and decompose within a year or two after they are formed. In contrast, woody tissues are much more durable, and may persist as part of a living tree for hundreds or even thousands of years before they die and gradually decompose.

Most compilations of global data that report total aboveground NPP, sometimes including belowground estimates, generally do not distinguish between leaf and wood production (e.g., Esser et al. 1997, Olson et al. 2001*a*, *b*). However, there are enough sites across the globe at which both leaf litterfall and woody biomass increment have been measured and estimated using similar methods (e.g., Cannell 1982), that general patterns can be identified (Fig. 9). It is apparent that the maximum mass of wood produced over a year in the tropical forests studied is roughly equivalent to the median amount of wood mass produced by the temperate forests that were studied (25–45° or higher). Although there is great variation within each latitudinal band, the highest maximum rates of annual wood

production, as well as the highest median rates, are found in temperate forests (Fig. 9).

The best documented latitudinal pattern in forest growth is the gradient of increasing leaf production from boreal forests of high latitudes to the rain forests of the tropics (Jordan 1971*a*, *b*, O'Neill and DeAngelis 1981, Proctor 1983, Vogt et al. 1986, Matthews 1997). This gradient has been thoroughly quantified by the simple method of litterfall collection (Jordan 1971*a*, *b*) and is dramatically illustrated by the seasonal patterns of greenness documented by satellite imagery. The year-round leaf cover of tropical rain forests results from an annual leaf production of approximately 5–8 Mg/ha over 12 months (Leigh 1999, Clark et al. 2001*b*), which is two to three times the mass of leaves produced by northern forests with a three- to six-month growing season.

The most striking productivity difference between tropical and temperate forests is in the ratio of leaf production to wood production. In none of the 14 tropical sites (Fig. 9) does the mass of wood produced exceed 50% of the total mass of wood plus leaves (i.e., total aboveground NPP). In contrast, at over half of the sites outside the tropics, wood production comprises over 50% of the aboveground NPP, and often substantially more. The ratio of wood production to total aboveground NPP is greatest in the range of 40–59° N latitude.

The primary significance of these results is that in tropical forests a much smaller proportion of net photosynthesis is used to produce wood than in temperate forests (Jordan 1971*a*, *b*). The proportion of aboveground NPP that is converted to long-term carbon storage as wood declines significantly across the latitudinal gradient from the poles to the equator (Fig. 9). A major difference in the productivity of tropical and temperate forests is that tropical forests produce a greater mass of leaves, both in absolute and relative terms, in relation to the amount of wood produced. Thus, for a given amount of NPP, tropical forests may actually have a lower rate of long-term carbon storage (net ecosystem production or NEP) and of tree growth rates than do temperate forests. This is consistent with the data that show lower basal area and lower rates of growth of rain forest trees, as indicated by their higher wood densities.

The relatively larger amount of leaf material produced by tropical forests does not necessarily translate into more food available for herbivores. Tropical plant leaves, especially of plants growing on poor soils, are well-known to be heavily defended by a number of different compounds that deter or injure herbivores (McKey et al. 1978, Gartlan et al. 1980, Coley et al. 1985, Coley 1987, Coley and Aide 1991, Coley and Barone 1996). This may help explain the relatively low density of insects in tropical systems in comparison to temperate systems on more fertile soils (e.g., Hails 1982; note that there are very few comparative studies of temperate and tropic insect abundance).

Advanced Methods for Estimating Forest NPP

The past few decades have seen the development of powerful satellite-based remote sensing systems, new computer models, and advanced methods of atmospheric chemical analysis that potentially allow quantification of net carbon dioxide exchange between the atmosphere and specific areas of land surface (e.g., Foley et al. 1998, DeFries et al. 1999, Running et al. 1999, El Saleous et al. 2000). A micro-meteorological method known as eddy–flux covariance (Baldocchi et al. 1988) measures changes in the CO_2 concentration of air as gusts or eddies move up or down over a forest or field. Summarizing differences in the CO_2 concentrations of upward vs. downward moving air masses allows calculation of the net flux between the vegetation and the atmosphere over time intervals ranging from a few minutes to an entire year.

The net carbon taken up by an area of vegetation does not correspond directly to NPP because it includes the respiration of carbon by microbes, invertebrates, and other organisms that consume plant material that may have been produced in the past, such as soil organic matter, as well as the current year's production of leaves, roots, and so on. The integration of data produced by eddy–flux covariance methods is called net ecosystem exchange (NEE) and will always be lower than NPP, because it subtracts losses due to both autotrophic and heterotrophic respiration, while NPP only subtracts autotrophic respiration. Nonetheless, net ecosystem exchange is generally considered to be correlated with net primary production (Pregitzer and Eukirchen 2004).

However, a potentially serious problem with eddy–flux measurements made in many regions is that nighttime atmospheric conditions are often too calm to produce the turbulence that maintains air exchange between the forest understory and the atmosphere. When this happens, the full amount of carbon released by nighttime autotrophic and heterotrophic respiration may not be measured. In some cases, the nighttime CO_2 near the forest floor may drain gravitationally off a site toward lower topographic positions (Loescher et al. 2006, Baldocchi 2008). This can result in an overestimate of NEE if major carbon losses at night are not subtracted from the carbon uptake by plants during the day (e.g., Saleska et al. 2003). A variety of such technical problems suggest caution when interpreting NEE estimates based on eddy–flux covariance (Clark 2004, Loescher et al. 2006, Baldocchi 2008).

A recent review of current eddy–flux estimates of NEE for forests and other ecosystems around the world (Baldocchi 2008), is based on a total of 506 full years of data distributed among 125 sites, including a few tropical sites. The global mean net annual CO_2 flux (F_N, in g $C \cdot m^{-2} \cdot yr^{-1}$) was −183 (median = −169, SD = 270). A negative value indicates uptake by the vegetation, positive values indicate release of CO_2 by the land surface, including vegetation. The largest uptake value reported in this analysis was slightly more negative than

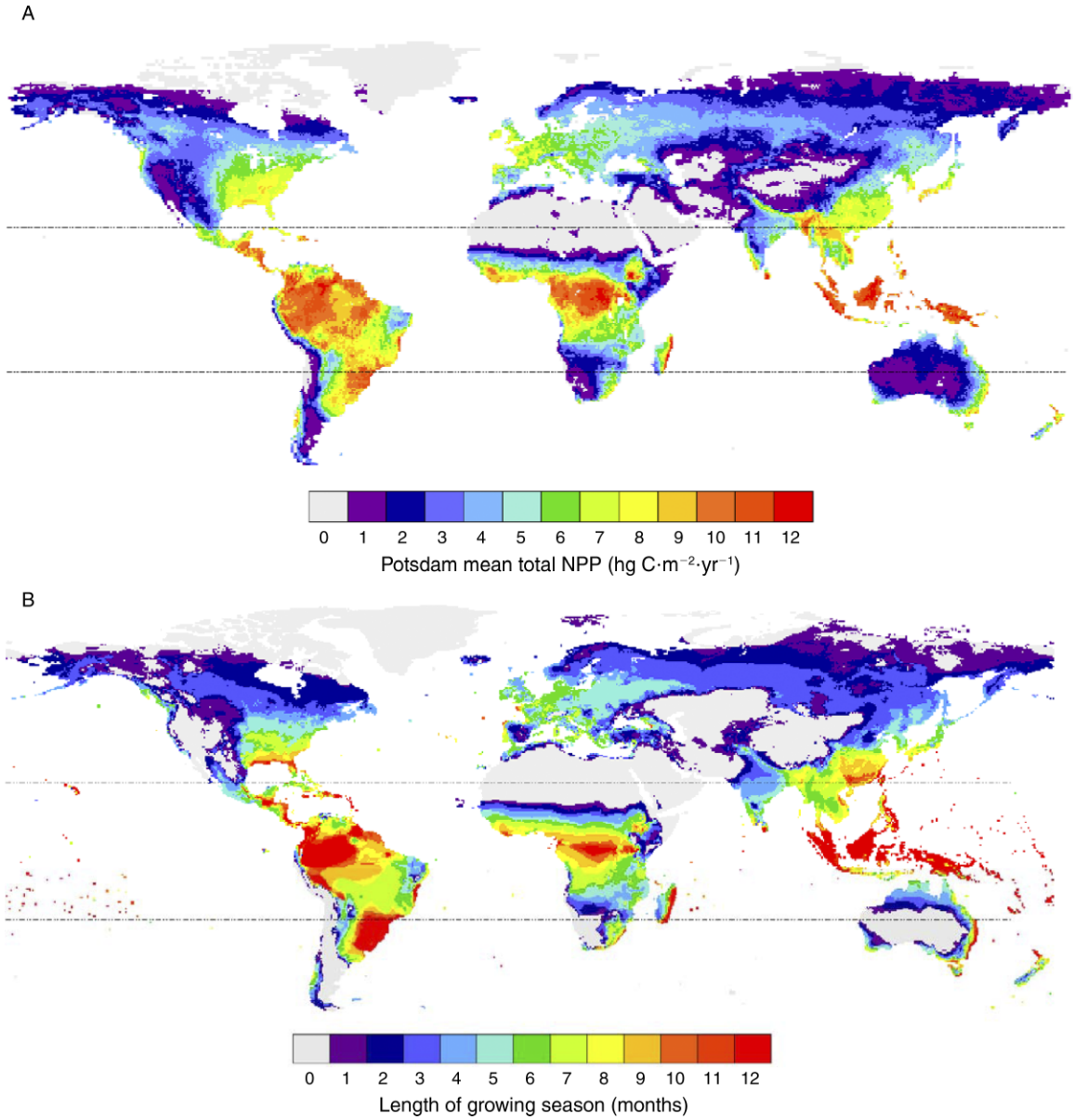

FIG. 10. (A) Average total NPP estimates of the 17 global vegetation models evaluated in the Potsdam Project (Cramer et al. 1999). Note that annual NPP values are in units of hectagrams (100 g) of carbon, which is approximately one-half of the biomass dry mass. (B) Global pattern of plant growing season, estimated from mean monthly climate data for the period 1961–1990 (New et al. 2000). See discussion in *The significance of short-term NPP rates in forest ecosystems.*

−1000. The highest annual values reported for tropical forests (−597 for Costa Rica [Loescher et al. 2003], −590 for Brazil [Mahli et al. 1998]) are within the range reported from temperate forests (Loescher et al. 2006). Given the potential problems with all of these data (Clark 2004, Loescher et al. 2006, Balcocchi 2008), as well as the large year-to-year, seasonal, and spatial variability reported in tropical forest NEE (Clark et al. 2003, Körner 2003, Loescher et al. 2003, Saleska et al. 2003), all of the eddy–flux data should be interpreted with caution, particularly where they conflict with traditional biometric estimates of NPP or NEP (see Curtis et al. 2002). Just as with biometric estimates of NPP, estimates of NEE are based on the subtraction of a very large number from a slightly larger (or slightly smaller) number. There are numerous opportunities for imprecision. In summary, the available eddy–flux measurements provide no support for the conclusion that tropical annual NEE is greater than temperate NEE and recent results suggest that annual rates of carbon sequestration in the tropics may have been consistently overestimated (Körner 2003, Saleska et al. 2003).

A second technological approach to estimating NPP, GPP, and other components of plant growth involves

the combination of satellite-derived information about forest leaf area with sophisticated computer models of plant growth (e.g., Potter et al. 1993, Field et al. 1998). A major effort to compare and summarize the output of numerous global vegetation models was published as a series of papers in 1999 (Cramer et al. 1999, Kicklighter et al. 1999, Ruimy et al. 1999, Schloss et al. 1999). Seventeen of these models, when averaged together, produced a global distribution of NPP that corresponded closely with published values for differences between the major biomes (e.g., Saugier et al. 2001) (Fig. 10A).

For comparison to the output of these complex models, Fig. 10B shows global variation in the length of the growing season for trees, which was estimated using the 1961–1990 0.5° gridded global mean monthly climatology (New et al. 1999, 2000). A simple algorithm was developed in which growing season length was limited by either low temperatures or low water availability. A month was counted in the growing season if the mean number of days with ground frost was less than or equal to five and if the mean monthly precipitation (mm/month) was greater than or equal to three times the average monthly temperature (°C). This precipitation algorithm is a simple approximation of potential evapotranspiration (PET) similar to that used in standard climate diagrams (Walter and Leith 1967). The temperature limitation affected primarily the temperate and boreal latitudes (Mikola 1962, Kozlowski et al. 1991), and the precipitation limitation affected primarily the temperate and tropical latitudes. These parameters produce a qualitative match with satellite-based estimates of tree cover (DeFries et al. 2000), with the frost-free growing period in the eastern United States (Koss et al. 1988), and with the computer-generated model estimates of global patterns of net primary production (Field et al. 1998, Cramer et al. 1999) (Figs. 1B and 10A).

A related approach, using earth surface color data generated by the MODIS (moderate resolution imaging spectroradiometer) satellite (Running et al. 2004), produces a very similar map to that of the Potsdam Project and the simple growing season algorithm. This is not surprising because all of the complex computer models of plant growth are based on the seasonal pattern of greenness over the planet, ranging from 12 months of leaf cover in the tropics to two or three months in the north temperate zone.

The Significance of Short-term NPP Rates in Forest Ecosystems

All of the above physical data, plus the few available eddy–flux measurements (but not the satellite greenness measurements or computer model predictions), are consistent with the interpretation that the total biomass and the annual aboveground NPP of tropical forests differs little from that of temperate forests, and may in fact be substantially lower.

While data on the carbon exchange of terrestrial ecosystems are typically summarized as annual totals because of their relevance to annual changes in atmospheric carbon dioxide concentrations, this may not be the most appropriate way to summarize these data for ecological and evolutionary issues. It is obvious that the time period during which plants are actually growing varies dramatically over the Earth, from 12 months near the equator, to a month or less at high latitudes and elevations (Fig. 10B). This seasonality affects marine NPP as well (Fig. 2). The global atmospheric effects of this seasonality in growth are illustrated by the dramatic three-dimensional graphs of temporal variation in atmospheric CO_2 concentrations across latitudes (Conway et al. 1994), and are reproduced to some degree by most global vegetation models (Bondeau et al. 1999, Kicklighter et al. 1999), because they are driven by satellite-based data on seasonal variation in leaf cover across the globe.

This seasonal variation in the rates of carbon uptake by plants is much more easily measured in marine/aquatic systems than in terrestrial systems. In marine/aquatic systems, all the biomass is directly involved in photosynthesis and growth, and NPP can be simply estimated as a direct correlate of chlorophyll concentration as it changes over the seasons (Fig. 2). However, in terrestrial systems, the growth and increase in stored carbon does not occur in the photosynthetic apparatus itself (the leaves), but rather in the trunks and branches, as well as in the unmeasurable belowground components. Because the storage of long-lived forms of biomass in the woody parts of trees is separated physically and temporally from the photosynthesis that occurs in the leaves, measurement of seasonal NPP in forests is much more difficult than in marine systems.

However, it seems likely that seasonal (or even monthly) NPP is more relevant to ecological and biogeochemical processes than annual NPP because it describes the rate of growth when plants are actually growing, taking up nutrients, transpiring water, and providing food for herbivores, etc. Knowing annual NPP in a boreal ecosystem with a three-month growing season provides no useful information about the rate of ecological processes in either the summer or the winter. Nor can annual boreal NPP give any insights into the maximum rates of biological activity in boreal vs. tropical ecosystems.

A simple estimate of monthly NPP while plants are growing can be made by dividing the annual total NPP at a specific location by the length of the growing season in months at that location. While more detailed and accurate time-series of NPP could be developed from detailed meteorological data or physiological measurements for each site in a global database, such data are typically unavailable.

Recent compilations of global climate data provide high resolution (e.g., 0.5° cells) estimates of major climatic parameters (New et al. 1999, 2000). These

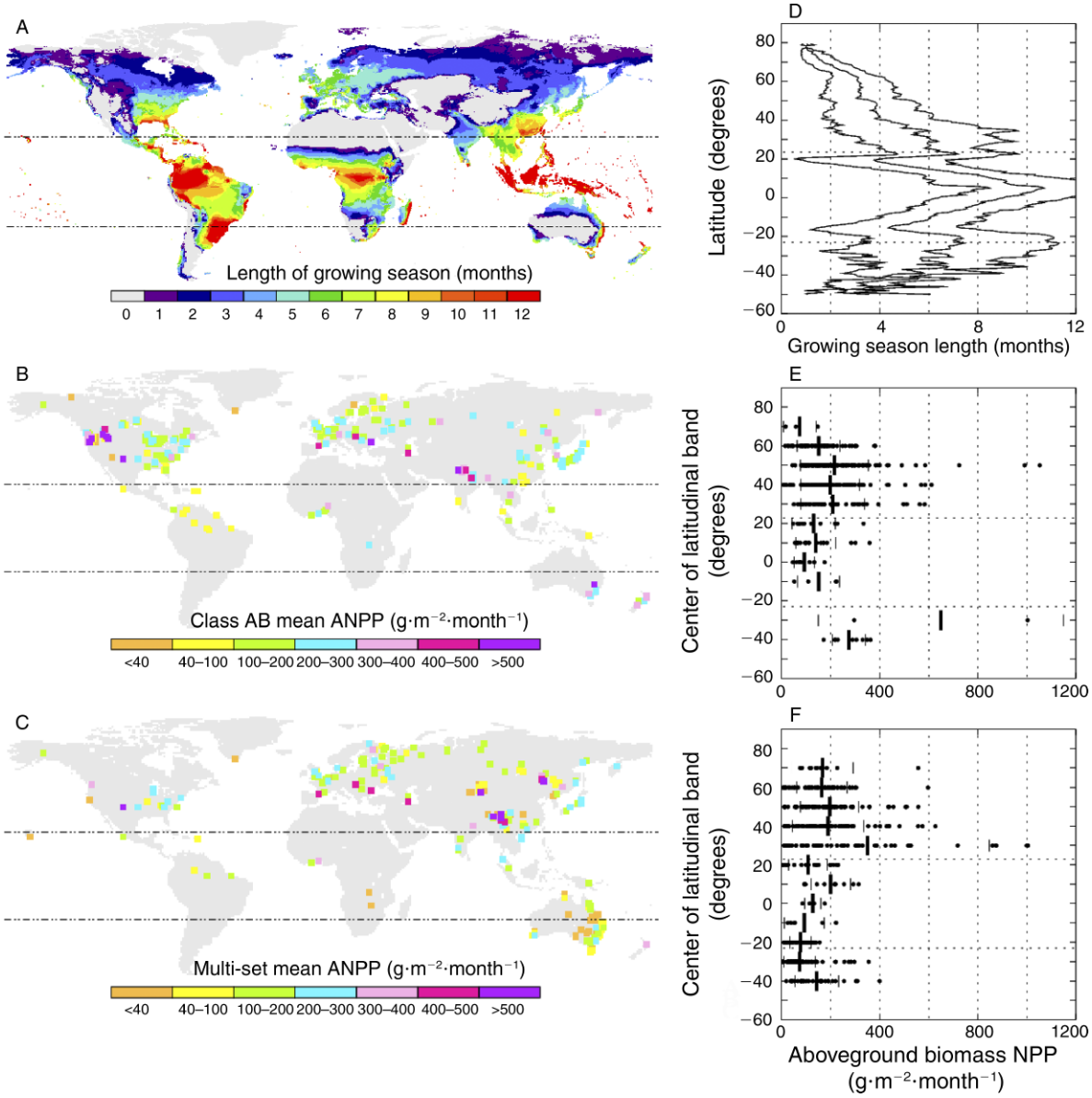

FIG. 11. Mean monthly rates of NPP during the growing season, an estimate of ecologically and evolutionarily relevant NPP (eNPP), based on (A) global patterns of plant growing season, estimated from mean monthly climate data for the period 1961–1990 (New et al. 2000); and site-specific monthly aboveground NPP (ANPP) estimates for forests around the world (minimum age of 100 years, where available) calculated by dividing annual ANPP (Fig. 6) by the estimated length of growing season in months (shown in A) for two compilations of data: (B) 362 class A and B sites from Olson et al. (2001*b*), and (C) 755 sites from a compilation of six historical data sets (see Fig. 6). Latitudinal patterns of (D) plant growing season by 1° bands (mean ± SD) and of monthly NPP aggregated by 10° bands (as described in Fig. 6) for two compilations of data: (E) 362 class A and B sites from Olson et al. (2001*b*) and (F) 755 sites from a compilation of six historical data sets (see Fig. 6)

parameters allow consistent global estimation of plant growing season (Fig. 10B), and thus allow standardization of annual NPP to monthly NPP averages during the growing season (Fig. 11B, C).

Conversion of total annual NPP to average monthly NPP reveals that the fastest monthly growth rates occur in the temperate zone, particularly the north temperate zone between 25° and 55°, where the mean values are nearly twice those in the tropics (Fig. 11E, F). Standardization of NPP by growing season length also reveals geographical patterns of NPP that are apparently related to soils and geological activity. The Pacific Northwest of North America, as well as the Himalayas and Tibetan Plateau, have noticeably greater monthly NPP values, as do New Zealand and southeastern Australia. Among the three major tropical regions, where NPP data are extremely sparse, South America apparently has lower monthly NPP than either Africa or Southeast Asia. This

is consistent with the distribution of soil fertility among these areas (Figs. 4 and 5), as well as with the greater wood density in South America (Fig. 8).

We refer to this short-term growing season NPP as "ecologically and evolutionarily relevant NPP," or eNPP (e.g., eANPP for the aboveground component, measured as either biomass or carbon in appropriate area and time units). While we would expect the average monthly eNPP during the growing season to be more closely related to the rates of plant growth and ecological and ecosystem processes than would be the total annual NPP, mean growing-season eNPP may not be the best predictor of the ecological responses of plants and animals to NPP. Most plants and animals time their life cycles, and particularly their reproduction, to the part of the year with optimal growing conditions, so that they will have the maximum amount of resources for reproduction. For many species this optimal period is a month or less, both in the tropics and the temperate zone. In order to understand the rates of the ecological and evolutionary processes that affect many types of plants and animals, it may make more sense to use the maximum monthly eNPP (or even weekly eNPP for species with extremely fast life cycle) as the primary indicator of the rates at which these processes occur. If this hypothesis about the regulation of growth rates proves valid, it means that the differences in the ecologically and evolutionarily relevant growth rates between tropical and temperate regions will be even greater than suggested in Fig. 11B, C.

An obvious prediction of the hypothesis that short-term eNPP is more important to animals than total annual NPP is that there should be strong correlations of the rates of animal growth and reproduction with latitudinal (or longitudinal, or any direction or scale) differences in eNPP. If the rates of eNPP are indeed greatest at high latitudes, the prediction is that rates of animal growth, reproduction, and related properties should also be greater at high latitudes than in the tropics.

Animal Responses to eNPP

Plants convert the carbon they fix to many different types of tissues, not all of which are edible for herbivores, and even the edible tissues vary in nutrient and energy content, as well as in the concentrations of toxic chemicals that deter herbivores (McKey 1974, 1980, McKey et al. 1978, Waterman et al. 1980, Coley et al. 1985, Coley 1987). Nonetheless, eNPP sets an upper bound on the food energy available to animals, so that in general, areas with high eNPP should be able to support larger herbivore population growth rates (secondary production) and greater total herbivore biomass than areas with low eNPP. This positive effect of eNPP on animal biomass should extend to higher trophic levels as well, such that predators, and insectivores such as birds, should also show a positive correlation between prey availability and total biomass (e.g., Carbone and Gittleman 2002). Consequently, animal biomass and secondary production should be highly correlated with eNPP.

Unfortunately, the prediction that total animal biomass should track variation in eNPP is almost impossible to test because of the difficulty of collecting reliable data on animal mass per unit area, as well as the rarity of having NPP data from areas where animals are studied in detail. Scattered data from lowland rain forest sites indicate an average biomass of terrestrial mammalian herbivores of 300 kg/km^2 (Fittkau and Klinge 1973, Terborgh et al. 1986, Bodmer 1989; summarized in Coley and Barone 1996) and for the more abundant arboreal herbivores a range of 450–1500 kg/km^2 (Leigh 1999). These lowland rain forest values are only 2–10% of the herbivore biomass typically found in high-productivity tropical grasslands and savannas (Talbot and Talbot 1963, Petrides and Swank 1965, 1966, Karanth and Sunquist 1992, Sinclair and Arcese 1995: Fig. 7.3).

As with plant NPP, we are forced to use surrogate variables that are more easily and frequently measured and that can be reasonably assumed to be correlated with total animal biomass per unit area. Perhaps the most promising surrogate variable is the body mass of individual animals. These data are extensively collected, and it is widely observed that animals grow more quickly and achieve larger body sizes where there is abundant food available (Teer et al. 1965, Boyce 1978, Kie et al. 1983, Langvatn and Albon 1986, Geist 1998, Meiri et al. 2007, Simard et al. 2008). The differences in body size between species are assumed to result in large part from selective pressures that are independent of local NPP, so that small rodents and elephants can both occur in the same environment. However, there are also patterns among closely related species, as well as among populations of a single species that are correlated with local environmental conditions and eNPP.

Individual organisms are typically larger in environments with more food. This is well known for animals with indeterminate growth, such as fish and reptiles, although variation in ages can confound comparisons of this type. However, animals with determinate growth may be even better surrogates, because they generally reach their maximum mature size within a few months to a few years, and this size is strongly influenced by food availability and growth rates during the immature stage (Calder 1984, Albon et al. 1987, Rogers 1987, Maehr and Moore 1992, Audo et al. 1995). A classic example is the variation in body size of white-tailed deer (*Odocoileus virginianus*) in North America, from the diminutive Key Deer of the rocky islands of the Florida Keys, to the robust deer of Midwestern agricultural areas.

While it is true that population density can affect body size through competition (Damuth 1981, 1991, Kie et al. 1983, Peters 1983, Blackburn et al. 1993, Cotgreave 1993, Currie and Fritz 1993, White et al. 2007,

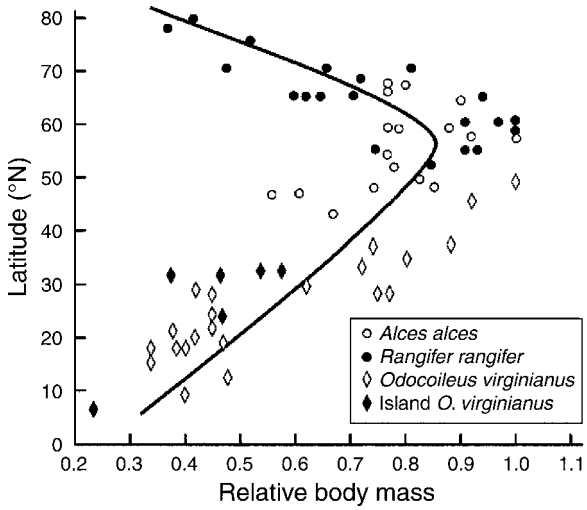

FIG. 12. Latitudinal gradient in relative body mass of cervids, showing intraspecific variation in white-tailed deer, moose, and caribou, as well as interspecific differences between the three species (from Geist 1998; reprinted by permission). Values for each species are derived from dividing the mass of each individual by the mass of the largest individual of that species.

Wolverton et al. 2007, Simard et al. 2008), it must also be true that there is some maximum body size that can be achieved in any given environment (Coe et al. 1976, Boyce 1978, Langvatn and Albon 1986, Mieri et al. 2007, Blois et al. 2008). Ultimately, constraints on foraging time and processing efficiency will allow animals to achieve larger individual sizes in environments with greater food availability (Coe et al. 1976, Boyce 1978, Guthrie 1984*a*, *b*, Geist 1987*a*, *b*, 1998, 1999, Gaston and Blackburn 1996, Ashton 2002, 2004), and there is evidence from African herbivores that the maximum local biomass of a species is positively correlated with the mean body mass for that species (Owen-Smith 1988: Fig. 14.2). Indeed, a recent consideration of geographic clines in body size related to Bergmann's rule contends that size relates to a variety of adaptive processes including interspecific competition (Diniz-Filho 2008), which clearly involves the availability of food.

Within North America, inter- and intraspecific variation in the body mass of cervids (deer, elk, moose, caribou, etc.) has a strong relationship with latitude (Fig. 12). Body size in cervids peaks at approximately 60° north latitude and declines at progressively higher latitudes. Geist (1987*a*, 1998) attributes this spatial variability in body size to differences in habitat productivity by latitude and argues that nutritious forage and silage are more abundant in temperate settings (see also Guthrie 1984*a*, *b*). It is in the tropics that cervids, specifically white-tailed deer, are the smallest, which suggests that secondary productivity mirrors global patterns in growing season forest productivity, that is, eNPP (Geist 1998) (Fig. 11E, F). Even within a single region, the south-central United States, body size of both modern and prehistoric deer is correlated with current agricultural productivity (Wolverton et al., *in press*). At the highest trophic level Geist (1987*a*) also demonstrates that body size in wolves (*Canis lupus*) mirrors the latitudinal trend in cervids.

Kennedy et al. (2002) provide evidence that is seemingly contrary to Geist's productivity–body-size relationship (which we will call "Geist's rule") for *Ursus americanus*. Black bear skull size is largest at low latitudes and decreases northward despite the fact that most of the black bear's range is south of 60° north latitude. Kennedy et al. (2002) propose the explanation for this pattern is that black bears hibernate in northern parts of their range but experience nearly year-round growth to the south, thus they have a longer growing season at southerly latitudes. However, Harlow (1962) found that although skull size in Florida black bears is relatively large, body mass is similar between Florida and Virginia conspecifics. At roughly the same latitude in Florida and Mexico, moreover, Maehr et al. (2001) found that bears in lower productivity habitat are relatively small in body size. Similarly, pre-extirpation historic-period black bear size in Missouri is relatively large, reaching the lower limits of late Pleistocene *U. americanus* (Wolverton and Lyman 1998, Wolverton 2008). Among brown bears (*U. arctos*) Meiri et al. (2007) found that body size is closely associated with proximity to food. It is important to note as well that the largest members of Ursidae occurred during the Pleistocene in temperate settings (Kurtén 1958, 1963, 1976, Kurtén and Anderson 1980, Stiner 1998, Grayson and Delpech 2003, Wolverton 2006) and the smallest members of the family today (*Helarctos malayanus*) inhabit tropical forests (Nowak and Paradiso 1983).

Another apparent exception to Geist's rule occurs in New World Felidae. The largest cat in the New World, the jaguar (*Panthera onca*), occurs in the tropics; however, we suggest that total jaguar biomass per unit area is likely to be substantially lower than for felids at temperate latitudes because the jaguar's population density is so low (Silver et al. 2004). The large home-range size of *P. onca* reflects low population density

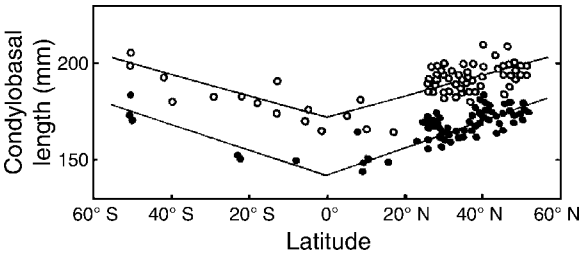

FIG. 13. Latitudinal gradient in skull size (condylobasal length of skull) of the mountain lion, *Puma concolor*. Open circles show males; solid circles show females. (The figure is from Kurtén [1973]; reprinted with permission of the Finnish Society of Sciences and Letters.)

(sensu Lindstedt et al. 1986) and a need to forage over large distances to meet energetic requirements. Further, at the intraspecific level, the puma (*Puma concolor*) increases in size with increasing latitude in both North America and South America from 0° to 60° north and south latitude (Kurtén 1973) (Fig. 13), which Iriarte et al. (1990) relate to corresponding increases in prey body size across the puma's range.

Meiri et al. (2004) document several exceptions to Bergmann's rule in Carnivora, although the majority of the taxa they examine support the rule (e.g., Rodríguez et al. 2006). If Geist's rule is the actual mechanism for latitudinal body size variation, then most species that follow Bergmann's rule should have latitudinal ranges that span low to mid latitudes (e.g., the puma [Kurtén 1973] and white-tailed deer [Geist 1987*a*]). Body size in taxa with ranges that span low to high latitudes should increase in body size to approximately 50–60° north latitude, where eNPP apparently reaches its maximum, and then decrease in size at progressively higher latitudes (e.g., Cervidae [Geist 1998], wolves [Geist 1987*a*], and tree squirrels [Heaney 1984]). Further, some exceptions to Geist's rule might be explained by latitudinal changes in behavioral ecology or might be the result of body mass being a less favorable proxy of secondary productivity than total animal biomass, which is unfortunately very difficult to quantify. Sufficient tests of Geist's rule, which is mechanistically independent of latitude and temperature, would include determination of body mass and population density in a species observed across areas that differ significantly in eNPP, with both intraspecific and interspecific contrasts.

Strong patterns in animal body size related to changes in latitude or altitude (and thus presumably productivity) also appear in other animals at scales ranging from global to insular (e.g., Hamilton 1961, Lindsey 1966, Chapman 1984, Kennedy and Lindsay 1984, Klein 1986, Langvatn and Albon 1986, Klein et al. 1987, Ritke and Kennedy 1988, Johnson 1998, Blackburn et al. 1999, Ashton 2002, Blackburn and Hawkins 2004, Greve et al. 2008, Guillaumet et al. 2008). Blackburn and Gaston (1996) report that the mean body mass of New World bird species is lowest in equatorial areas, and increases with latitude to the north and south. Specifically, this pattern is strong for Anseriformes (ducks and geese; Gaston and Blackburn 1996) and Andean Passeriformes (perching birds; Graves 1991). Interestingly, there is an inverse correlation between mean body mass and the species richness of birds in a given area, which is stronger than the correlation of either variable with latitude (Blackburn and Gaston 1996). The same data showed only a very weak relationship between mean body mass and mean geographic range size. The positive relationship between body size and latitude extends to many other bird taxa as well and appears to be independent of phylogeny (James 1970, Ashton 2002).

Chown and Klok (2003) document that Antarctic insular insects increase in body size with altitude in settings where food availability does not decrease at higher elevations. Not surprisingly, insect body size decreases with altitude in settings where resource availability decreases at higher elevations.

While population density potentially affects body size and could confound tropical–temperate comparisons, Johnson (1998) found that population densities of Australian mammals (comparing 69 species) were lower in the tropics, where both geographical range sizes and body sizes were also smaller. For 13 species with ranges that included the tropical and temperate zones, he found that population densities tended to be greater in the temperate portion of their range, and that for some of the species body size also increased in the temperate portion. On average, based on body size and population density, he estimated that the "tropical populations used about one order of magnitude less energy than did temperate populations of the same species" (Johnson 1998:692). In our opinion, the latitudinal distribution of NPP as a potential cause of body size variation has been overlooked precisely because the global distribution of eNPP is not clearly understood. If temperate latitudes are relatively higher in eNPP, then body size increases with increasing latitude are more easily explained.

Reproduction is a critical component of population dynamics that is directly related to the amount of resources available in the environment. It has long been known that clutch sizes in birds are larger in the temperate regions than in the tropics (Lack 1947, 1948, 1968). More recent data show that the number of young that are successfully fledged is also correlated with latitude, reaching a maximum between 50° and 60° north latitude before declining toward the poles (Sanz 1997, 1998). Koenig (1986) found that clutch size and latitude are positively correlated at both the intra- and interspecific levels in North American woodpeckers.

Increases in clutch and litter size with latitude and/or altitude are apparent across multiple biological taxa including birds (Johnston 1954, Hussell 1972, Payne 1976, Skutch 1985, Young 1994, Martin et al. 2000), non-hibernating mammals (Lord 1960, Barkalow 1962, Smith and McGinnis 1968, Spencer and Steinhoff 1968, Kilgore 1970, Cockburn et al. 1983, Heaney 1984, Virgós et al. 2006), crustaceans (Poulin 1995, Poulin and Hamilton 1995), and fish (Fleming and Gross 1990). Many of the same studies, however, describe corresponding decreases in egg size, offspring size, and/or number of clutches or litters per annum with latitude such that as clutch/litter size increases, energy invested per offspring decreases, This implies a shift from *K*- to *r*-selection in reproductive effort from the tropics to the temperate regions, which is consistent with the shift from lower to higher resource availability suggested by our reevaluation of the latitudinal gradient of terrestrial NPP.

Nestling bird growth rates are also known to have a tropical–temperate gradient, with faster growth rates in the temperate zone. Nestlings are fed primarily insects,

which are more abundant when eNPP and plant palatability are high. This pattern has been documented in interspecific comparisons of similarly-sized congeners (Ricklefs 1976, 1983), as well as between tropical and temperate subspecies of the black swift, in which the temperate subspecies weighs 25% more than the tropical subspecies (Marin 1999), which contradicts the generalization that smaller birds grow faster, all other factors being equal (Ricklefs 1983).

Not surprisingly, at very high latitudes and altitudes, litter or clutch size in some taxa decline (Murie et al. 1980). At any particular latitude a diverse set of mechanisms may influence variability in clutch and litter size, including nest visitation rates related to predation risk (Lima 1987, Martin et al. 2000), diversity in local food availability (Perrins 1965, Stenseth et al. 1985, Young 1994, Korpimäki and Wiehn 1998), seasonal restrictions on breeding periods (Spencer and Steinhoff 1968), energetic and/or anatomical constraints during lactation in mammals (Millar 1978, Cockburn et al. 1983, Glazier 1985), and multiple factors related to increased parental and offspring mortality across diverse environmental settings (e.g., Lima 1987, Rotenberry and Wiens 1989, Young 1994). However, none of these mechanisms fully explains the broader geospatial patterns in the reproductive biology of animals, which we interpret as related more closely to global patterns in eNPP.

Fewer data are available for the most abundant animals on the planet, insects. As the dominant consumers of living and dead plant material on the planet, they would be expected to respond directly to variation in eNPP. Within the Amazon basin, Radtke et al. (2007) found that dung beetle volume and abundance were significantly greater (over two times, and nearly four times, respectively) on more fertile, young soils in western Amazonia than on infertile, old soils in central Amazonia. Similar spatial variation was found in the Appalachian forests of North America, where both macroinvertebrate biomass and the reproductive success of the Ovenbird (*Seiurus aurocapillus*) were positively correlated with forest productivity, estimated using forestry site index (Seagle and Sturtevant 2005). Two studies that looked at egg production rates in insects found that rates increase from tropical to temperate regions (Landahl and Root 1969, Peschen 1972).

Unfortunately, while there are numerous studies of insect diversity in tropical forests (Erwin and Scott 1980, Erwin 1982, 1983, 1988), there are few data for latitudinal comparisons of insect biomass. One of the few quantitative tropical–temperate comparisons was carried out by Hails (1982), who used a suction trap to capture flying insects over the course of a year in Scotland and Malaysia (Fig. 14). The maximum growing-season insect biomass in Scotland was 10 times larger than in Malaysia.

Such differences in insect biomass between tropical and temperate forests should result in significant

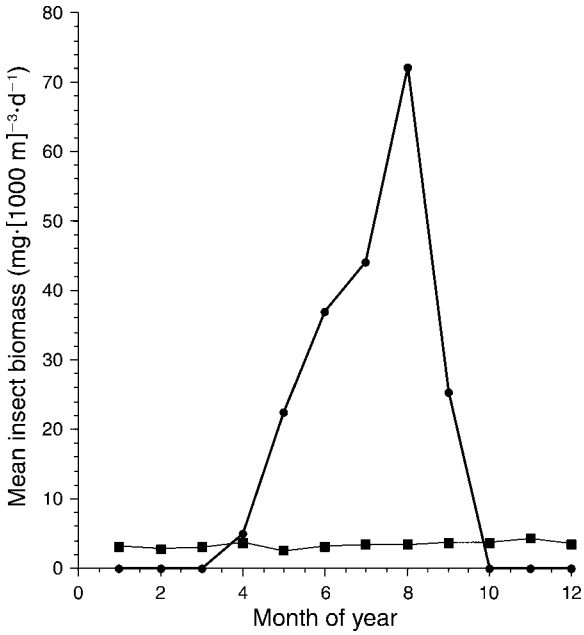

FIG. 14. Monthly mean aerial insect biomass from suction traps 1.8 m above ground surface in parkland habitat adjacent to wooded areas at the University of Malaya, Kuala Lumpur, 3° N (circles), and the University of Stirling, Scotland, 57° N (squares) (based on Hails [1982]).

differences in food availability for insectivores. A comparison of the foraging efficiency of small foliage-gleaning passerines in broad-leafed forests in France and French Guiana (Thiollay 1988) found that the food capture rates in the temperate forest were three times greater than in the tropical forest. This is consistent with other studies that found slow growth (Ricklefs 1976, 1983) and starvation of young in tropical birds, for which foraging occupied as much as 90% of the daily time budget (Drycz 1985, Marcotullio and Gill 1985). "Contrary to the widely assumed superabundance and stability of food resources in the tropics, it is suggested that a reduced prey availability (density, detectability, distribution, seasonality) may be a major cause of the lower foraging success of rain forest birds. Accordingly, this constraint is likely to limit their reproductive rate and would in part explain their very low clutch size" (Thiollay 1988:17).

Non-latitudinal differences in clutch size have also been described in contrasts between different habitat types that are clearly related to differences in eNPP (e.g., Snow 1958, Lack and Moreau 1965, Klomp 1970, Wooller et al. 1985). Although Korpimäki and Wiehn (1998) did not relate clutch size in Eurasian Kestrels (*Falco tinnunculus*) to latitude, they conclude that annual fluctuations in food availability drive clutch sizes in western Finland. Among South American passerines Yom-Tov et al. (1994) found no relationship between clutch size and latitude; although they found that clutch size was low in the Amazon compared to other areas of

South America. They linked relatively low clutch size in the southern hemisphere to Ashmole's (1961, Koenig 1986) hypothesis that clutch size is influenced by factors related to seasonality and reproduction, in this case lower migration frequency and milder winter climate in South America than in North America. Yom-Tov et al. (1994) hypothesized that competition among conspecifics should be high in South America because relatively low migration-related mortality leads to higher population densities and a situation in which individuals cannot feed large clutches. Thus, they conclude that small clutch size in South America is a product of low food availability per parent and offspring, although their proposed mechanism is based on the unsubstantiated assumption of high population densities, which is not consistent with our hypothesis of low productivity.

Although Yom-Tov et al. (1994) state that northern species migrate south to *avoid* winter; we suggest a different direction of causality. We hypothesize that tropical species migrate north to *take advantage of* the high seasonal productivity (eNPP) at temperate latitudes during reproduction. In our interpretation, the relatively uniform latitudinal distribution of small clutch sizes in South America reflects the overall lower monthly primary and secondary productivity in this part of the tropics as compared to the temperate regions of the northern hemisphere. Note that differences in soil fertility and eNPP among the three major rain forest regions should result in different selective advantages for migrating to the temperate zone to breed.

In summary, body size, density, and reproductive biology patterns in a wide range of animals do not support the conclusion that either secondary production or net primary productivity is greatest in the tropics. As with body size, latitudinal patterns in reproductive efficiency suggest that rates of ecologically relevant secondary (and thus primary) productivity are substantially higher in the temperate zone.

Discussion

All of the available data on forest structure and productivity, and much of the data on animal body size and reproduction, are inconsistent with the current belief that tropical forests have more biomass and are more productive than temperate forests, at any time scales. In fact, the highest short-term rates of NPP (eNPP) apparently occur in temperate and boreal forests.

These patterns of forest productivity are consistent with the global distribution of soil fertility, as well as the productivity of certain types of crops and the standardized economic value of agricultural production (Huston 1993, 1994). If correct, this interpretation of global forest mass and productivity patterns has major implications for understanding the global carbon cycle, the stability and resilience of ecosystem processes (Huston 1997:451–453), sustainable management of renewable resources, the evolution of many aspects of the Earth's biodiversity, including the latitudinal gradient of species diversity, and the migratory patterns of terrestrial birds and marine vertebrates. A reevaluation of many ecological concepts may be needed.

In addition to their implications for the global carbon cycle, wood and leaf production rates also have differing implications for ecological processes and human activities. Clearly, wood production, not total NPP, is the critical issue for forestry, as well as for forest succession, in which more rapid growth to a large height often confers an insurmountable advantage in competition for light. However, leaf production rate is more critical for organisms that feed on leaves, such as herbivorous insects and mammals. The greater annual leaf production in the tropics could potentially have a major positive impact on the population sizes and diversity of herbivorous animals, were it not for several additional factors.

Because the greater leaf production in tropical rain forests occurs continuously over a growing season that is two to three times longer than in temperate regions, the maximum amount of new leaf production that is available to herbivores on a short-term basis is actually larger in temperate and boreal forests where the production of new leaves is concentrated into a period of a few months (Geist 1998:15). In addition, the digestibility and nutritional quality of the leaves of slowly-growing tropical trees are often much lower than that of the leaves in temperate forests. The higher concentration of anti-herbivore "secondary chemicals" in tropical leaves is well known, and explained as a response to both the low levels of soil nutrients in many tropical soils, and to the need to protect leaves against herbivores (McKey et al. 1978, Gartlan et al. 1980, Waterman et al. 1980, Coley et al. 1985, Coley 1987).

This concentration of leaf production into a short period in temperate climates results in a higher availability of food for insects, which are able to respond much more rapidly to the spring burst of productivity than larger herbivores, such as mammals. Consequently, insect populations in the temperate zone can reach much greater abundance than in most lowland tropical forests (Fig. 14). This pulse of insect abundance is almost certainly the primary reason that many bird species migrate from tropical forests to the temperate zone to breed, just as diadromous fish feed in the most productive environment available, whether freshwater or marine (Gross et al. 1988). A remarkable, recently discovered marine example of a response to the tropical-temperate productivity gradient is the Hawaiian Petrel (*Pterodroma sandwichensis*), a tropical seabird that nests in montane forests in Hawaii, and makes two-week long 10 000 km foraging trips to the productive waters of the north Pacific to catch food for its young in Hawaii (J. Adams, *unpublished data*). There are several other seabirds, including the Slender-billed Shearwater or Australian Muttonbird (*Puffinus tenuirostris*), the Sooty Shearwater (*Puffinus griseus*), and the Arctic Tern

PLATE 1. *Cecropia* and other early successional rainforest tree species as seen from the La Selva Biological Station in the Caribbean lowlands of Costa Rica in 1978. Photo credit: M. A. Huston.

(*Sterna paradisea*) that migrate seasonally between subantarctic and subarctic waters to feed (Austin 1961, Minami and Ogi 1997, Spear and Ainley 1999, Bovy 2007).

For Neotropical migrants that nest in forests, the high energy costs and risk of mortality associated with long distance migration must be exceeded by the reproductive benefit gained by raising young in the more productive temperate forests, rather than in tropical forests. Thus, neotropical and paleotropical migrants and other latitudinally migrating birds can be interpreted as tropical species that fly north in order to obtain more food and reproduce more successfully, rather than as temperate species that fly south to avoid winter (e.g., Yom-Tov et al. 1994). This is clearly analogous to the shorter distance migration of large mammals that move to areas of higher eNPP caused by predictable variation in rainfall or other aspects of seasonality in grasslands and savannas.

This "reversal" of the presumed latitudinal pattern of terrestrial plant productivity has major implications for understanding the causes of the latitudinal gradient of species diversity. Most of the ecological and evolutionary theories about species diversity (e.g., energy–diversity theory, niche partitioning, diversity–stability) were developed under the assumption that the high diversity of tropical rain forests was the consequence of their greater productivity, as well as their presumed greater temporal stability in relation to temperate environments. If the ecologically and evolutionarily relevant productivity of tropical forests is actually lower than in temperate forests, this provides support for an alternative group of ecological theories that relate high diversity to low productivity, particularly for plants (Patrick and Strawbridge 1963, Rosenzweig 1971, Grime 1973, 1979, Huston 1979, 1980, 1994).

"Reversal" of the latitudinal gradient of productivity would also contribute to the conceptual unification of ecological, ecosystem, and evolutionary science by reconciling the apparently opposing patterns of marine and terrestrial productivity and the resources and processes that regulate species diversity. Marine nutrients are derived from the same source as the mineral nutrients of soils, creating a previously unrecognized positive correlation between terrestrial and marine productivity, both of which tend to be greater where fresh minerals are exposed by glaciation, volcanic activity, and erosion of young mountain ranges. The positive correlation between marine and terrestrial biodiversity can now be interpreted as the result of a set of processes that are affected similarly by NPP, so that biodiversity is highest where eNPP is relatively low.

Patterns caused by the influence of mineral nutrient availability on plant productivity, as well as on plant

and animal species diversity, can be found at much smaller scales than the latitudinal gradient, as a consequence of the structure of hydrologic drainage networks interacting with climate and geology (e.g., Rodríguez-Iturbe and Rinaldi 1997). Both tropical and temperate forests have similar topographic patterns of large tree size, faster tree growth rates, and lower tree diversity in valleys and riparian areas with nutrient-rich alluvial soils that contrast with hillsides and ridges that have poorer soils and may be somewhat drier but typically have higher tree diversity. Variation in soil nutrients is associated with patterns of forest structure and diversity over multiple scales (Holdridge et al. 1971, Hall and Swaine 1976, Huston 1980, Clark et al. 1998, Laurance et al. 1999, Baker et al. 2004, Phillips et al. 2004), up to the global pattern of soil fertility (Huston 1993, 1994).

One question that cannot be avoided is how we got this major pattern so wrong, for so long. Certainly, early misconceptions about the "exuberant growth" of tropical rain forests (e.g., Dobzhansky 1950) helped shape the dogma about the latitudinal gradient of NPP. This dogma was embraced by nearly everyone, and ensnared theoreticians as well, who developed theories to explain the ecological and evolutionary processes that caused the more productive tropics to have the highest species diversity. The contradictory data and interpretations that were presented (e.g., Jordan 1971*a*, *b*, Meggers 1971, Huston 1979, 1980, 1993, 1994, Huston et al. 2000, Cramer et al. 2001: Table 18-2, Olson et al. 2001*a*) were basically ignored. It may be significant that some studies have suggested that there is an unexpectedly large "carbon sink" (carbon removed from the atmosphere by NPP) in the northern forests (Enting and Mansbridge 1991, Ciais et al. 1995, 2000, Enting 2000, Myneni et al. 2001) and a much smaller sink in Amazonian forests than previously thought (Ciais et al. 2000, Saleska et al. 2003), but this has not led to a reevaluation of global patterns of NPP (e.g., Running et al. 2004).

Even more perplexing is the output of the global vegetation models, all of which consistently predict that total NPP is much greater in the tropics (Field et al. 1998, Cramer et al. 1999, Kicklighter et al. 1999, Potter 1999). An insight into the operation of these models is provided by Fig. 10, which compares the mean output of 17 global vegetation models (Fig. 10A) to a map of estimated woody plant growing season based on gridded global climate data (Fig. 10B). The strong similarity of the simple two-parameter growing season map (Fig. 10B) with the output map of the complex multi-factor physiological vegetation models suggests that most of the pattern produced by these complex models is based on variation in the length of the growing season, with an average NPP of approximately 100 g C/m^2 per month across all terrestrial ecosystems (cf. Schloss et al. 1999).

This global uniformity of model-generated instantaneous (e.g., monthly) NPP (which is equivalent to eNPP) is not surprising given that the models do not include the effect of soil nutrients on plant growth and NPP (e.g., Fig. 4A), and may not adequately represent the limitations on plant growth imposed by poor soils and high respiration rates under warm conditions. The growth equation for the Carnegie-Ames-Stanford approach (CASA) model is: $\mathrm{NPP} = f(\mathrm{NDVI}) \times \mathrm{PAR} \times \varepsilon^* \times g(\mathrm{T}) \times h(\mathrm{W})$, where NDVI is the satellite-derived greenness index, PAR is incoming photosynthetically active solar radiation, ε^* is a function of the "maximum achievable light utilization efficiency adjusted by functions that account for the effects of temperature $g(\mathrm{T})$ and water stress $h(\mathrm{W})$" (Field et al. 1998). This focus on the direct effects of temperature and precipitation on photosynthesis and growth, without any consideration of the effects of nutrients on ε^*, is similar to the Miami model, which was the first global vegetation model (Lieth 1975). This may be one of the reasons that these models make predictions that are almost the complete opposite of the observations summarized in this paper. A recent analysis suggests that some of the global vegetation models may have overestimated NPP, and that the predictions of different models vary by a factor as great as two (Hoffman et al. 2007).

Recognition that ecologically relevant productivity, eNPP, is effectively greater in the temperate zone than in the tropics should obviate the convoluted arguments that have been developed to explain why temperate organisms often have faster growth rates (r) than tropical organisms, but tropical organisms do not have compensatory larger carrying capacities (K) than temperate organisms (e.g., Cody 1966, Ricklefs 1970, Price 1974). This also helps explain why tropical birds leave the rain forest to migrate thousands of miles so they can raise their young in temperate forests (Yom-Tov et al. 1994). Theories to explain the decreasing clutch sizes from temperate to tropical systems on the basis of conditions during the nonreproductive season (e.g., Ricklefs 1980) are probably unnecessary. Similarly, the widely known, but somewhat controversial "Bergmann's rule" (Bergmann 1847, Meiri et al. 2004, Diniz-Filho 2008) that animal body size increases with latitude because colder temperatures favor the smaller surface-to-volume ratio of large body size, might now be interpreted as the straightforward effect of food availability on body size (Geist 1987*a*, *b*, 1998, 1999). There is no known latitudinal gradient of disturbance frequencies that could explain the differences between tropical and temperate forests (e.g., Connell 1978), but there is a clear global gradient of soil fertility, and apparently also eNPP, that potentially could explain these differences.

If the pattern of terrestrial eNPP reported here is confirmed by more extensive and complete measurements, it will necessitate a reevaluation of current global carbon models, as well as of many elements of ecological and evolutionary theory that were developed under the assumption that tropical forests had greater biomass

and were more productive than temperate forests (e.g., Connell and Orias 1964, Connell 1978, Wright 1983, Cousins 1989, Rosenzweig 1995, Francis and Currie 1998, Kleidon and Mooney 2000, Hubbell 2001, Hawkins et al. 2003, Willig et al. 2003, Currie et al. 2004, Mittelbach et al. 2007). Furthermore, global policies related to sustainable development, forestry, agriculture, and conservation of biodiversity and other natural resources should also be reexamined, as should the relationship between soils, biodiversity, and poverty (Huston 1993, 1994, 2005).

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Literature Cited

Aber, J. D., and J. M. Melillo. 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. Canadian Journal of Botany 58: 416–421.

Ajtay, G. L., P. Ketner, and P. Duvigneaud. 1979. Terrestrial primary productivity and phytomass. Pages 129–182 *in* B. Bolin, E. T. Deggens, S. Kempe, and P. Ketner, editors. The global carbon cycle, SCOPE 13. John Wiley and Sons, New York, New York, USA.

Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density dependent effects and cohort variation. Journal of Animal Ecology 56:69–81.

Alden, H. A. 1995. Hardwoods of North America. General Technical Report, FPL-GTR-83. USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin, USA.

Alden, H. A. 1997. Softwoods of North America. General Technical Report, FPL-GTR-102. USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin, USA.

Anderson, D. E., A. S. Goudie, and A. G. Parker. 2007. Global environments through the Quaternary: exploring environmental change. Oxford University Press, Oxford, UK.

Araujo, T. M., N. Higuchi, and J. Andrade de Carvalho, Jr. 1999. Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Para, Brazil. Forest Ecology and Management 117:43–52.

Ashmole, N. P. 1961. The biology of certain Terns. Dissertation. Oxford University, Oxford, UK.

Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecology and Biogeography 11:505–523.

Ashton, K. G. 2004. Sensitivity of intraspecific latitudinal clines of body size for tetrapods to sampling, latitude and body size. Integrative and Comparative Biology 44:403–412.

Audo, M. C., T. M. Mann, T. L. Polk, C. M. Loudenslager, W. J. Diehl, and R. Altig. 1995. Food deprivation during different periods of tadpole (*Hyla chrysoscelis*) ontogeny affects metamorphic performance differently. Oecologia 103: 518–522.

Austin, O. L., Jr. 1961. Birds of the world: a survey of the twenty-seven orders and one hundred and fifty-five families. Golden Press, New York, New York, USA.

Baker, T. R., et al. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10:545–562.

Baldocchi, D. D. 2008. "Breathing" of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. Australian Journal of Botany 56:1–26.

Baldocchi, D. D., B. B. Hicks, and T. P. Meyers. 1988. Measuring biosphere–atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology 69: 1331–1340.

Barkalow, F. S., Jr. 1962. Latitude related to reproduction in the cottontail rabbit. Journal of Wildlife Management 26:32–37.

Barrett, D. J. 2001. NPP multi-biome: VAST calibration data, 1965–1998. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. ⟨http://www.daac.ornl.gov/⟩

Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, P. G. Falkowski, R. M. Letelier, and E. S. Boss. 2006. Climate-driven trends in contemporary ocean productivity. Nature 444:752–755.

Behrenfeld, M. J., J. T. Randerson, C. R. McClain, G. C. Feldman, S. O. Los, C. J. Tucker, P. G. Falkowski, C. B. Field, R. Frouin, W. E. Esaias, D. D. Kobler, and N. H. Pollack. 2001. Biospheric primary production during an ENSO transition. Science 291:2594–2597.

Bergmann, C. 1847. Über die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien, Göttingen 3: 595–708.

Bishop, J. K. B., R. E. Davis, and J. T. Sherman. 2002. Robotic observations of dust storm enhancement of carbon biomass in the North Pacific. Science 298:817–821.

Black, K. D., and G. B. Shimmield, editors. 2003. Biogeochemistry of marine systems. Blackwell, Oxford, UK.

Blackburn, T. M., V. K. Brown, B. M. Doube, J. J. D. Greenwood, J. H. Lawton, and N. E. Stork. 1993. The relationship between abundance and body-size in natural animal assemblages. Journal of Animal Ecology 62:519–528.

Blackburn, T. M., and K. J. Gaston. 1996. Spatial patterns in the body sizes of bird species in the New World. Oikos 77: 436–446.

Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distributions 5:165–174.

Blackburn, T. M., and B. A. Hawkins. 2004. Bergmann's Rule and the mammal faunal of northern North America. Ecography 27:715–724.

Blois, J. L., R. S. Feranec, and E. A. Hadly. 2008. Environmental influences on spatial and temporal patterns of body-size variation in California ground squirrels (*Spermophilus beecheyi*). Journal of Biogeography 35:602–613.

Bodmer, R. E. 1989. Ungulate biomass in relation to feeding strategy within Amazonian forests. Oecologia 81:547–550.

Bolza, E., and N. H. Kloot. 1963. The mechanical properties of 174 Australian timbers. Technological Paper No. 25. Division of Forest Products, CSIRO, Melbourne, Australia.

Bondeau, A., D. W. Kicklighter, and J. Kaduk, the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. Global Change Biology 5(Supplement 1):35–45.

Bovy, K. M. 2007. Global human impacts? Explaining the Sooty Shearwater decline at the Minard site, Washington State, USA. Journal of Archaeological Science 34:1087–1097.

Boyce, M. S. 1978. Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. Oecologia 36:1–19.

Brady, N. C., and R. R. Weil. 2002. The nature and properties of soils. 13th Edition. Prentice-Hall, Engelwood Cliffs, New Jersey, USA.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. Cid Ferreira, and R. A. Victoria. 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. Forest Ecology and Management 75: 175–189.

Brown, S. 1997. Estimating biomass and biomass change of tropical forests. FAO Forestry Paper 134. Food and Agriculture Organization of the United Nations, Rome, Italy.

Brown, S. 2002. Measuring carbon in forests: current status and future challenges. Environmental Pollution 116:363–372.

Brown, S., and G. Gaston. 1995. Use of forest inventories and geographic information systems to estimate biomass density of tropical forests: application to tropical Africa. Environmental Monitoring and Assessment 38:157–168.

Brown, S., L. R. Iverson, A. Prasad, and D. Liu. 1993. Geographical distributions of carbon in biomass and soils of tropical Asian forests. Geocarta International 4:45–59.

Brown, S., and A. E. Lugo. 1984. Biomass of tropical forests: a new estimate based on forest volumes. Science 223:1290–1293.

Brown, S., and A. E. Lugo. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17:8–18.

Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. Oecologia 111:1–11.

Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press, Cambridge, Massachusetts, USA.

Cannell, M. R. G. 1982. World forest biomass and primary production data. Academic Press, London, UK.

Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science 295:2273–2276.

Chapman, J. A. 1984. Latitude and gestation period in New World rabbits (Leporidae: *Sylvilagus* and *Romerolagus*). American Naturalist 124:442–445.

Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easdale, H. ter Steege, and C. O. Webb. 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecological Applications 16:2356–2367.

Chown, S. L., and C. J. Klok. 2003. Altitudinal body size clines: latitudinal effects associated with changing seasonality. Ecography 26:445–455.

Chudnoff, M. 1979. Tropical timbers of the world. USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin, USA.

Ciais, P., P. Friedlingstein, A. Friend, and D. S. Schimel. 2001. Integrating global models of terrestrial primary productivity. Pages 449–487 *in* J. Roy, B. Saugier, and H. A. Mooney, editors. Terrestrial global productivity. Academic Press, San Diego, California, USA.

Ciais, P., P. Peylin, and P. Bousquet. 2000. Regional biospheric carbon fluxes as inferred from atmospheric CO_2 measurements. Ecological Applications 10:1574–1589.

Ciais, P., P. P. Tans, J. W. C. White, M. Trolier, R. J. Francey, J. A. Berry, D. R. Randall, P. J. Sellers, J. G. Collatz, and D. S. Schimel. 1995. Partitioning of ocean and land uptake of CO_2 as inferred by $\delta^{13}C$ measurements from the NOAA Climate Monitoring and Diagnostics Laboratory global air sampling network. Journal of Geophysical Research 100: 5051–5070.

Clark, D. A. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. Ecological Applications 12:3–7.

Clark, D. A. 2004. Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. Philosophical Transactions of the Royal Society London B. 359:477–491.

Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Tomlinson, and J. Ni. 2001*a*. Measuring net primary production in forests: concepts and field methods. Ecological Applications 11:356–370.

Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Tomlinson, J. Ni, and E. A. Holland. 2001*b*. NPP in tropical forests: an evaluation and synthesis of existing field data. Ecological Applications 11:371–384.

Clark, D. A., S. C. Piper, C. D. Keeling, and D. B. Clark. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proceedings of the National Academy of Sciences (USA) 100:5852–5857.

Clark, D. B., D. A. Clark, and J. M. Read. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. Journal of Ecology 86:101–112.

Cleveland, C. C., and A. R. Townsend. 2006. Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. Proceedings of the National Academy of Sciences (USA) 103:10316–10321.

Cockburn, A., A. K. Lee, and R. W. Martin. 1983. Macrogeographic variation in litter size in *Antechinus* (Marsupialia: Dasyuridae). Evolution 37:86–95.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174–184.

Coe, M. J., D. H. Cumming, and J. Phillipson. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. Oecologia 22:341–354.

Coley, P. D. 1987. Interspecific variation in plant antiherbivory properties: the role of habitat quality and rate of disturbance. New Phytologist 106(Supplement):251–263.

Coley, P. D., and T. M. Aide. 1991. A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pages 25–49 *in* P. W. Price, T. M. Lewinson, G. W. Fernandes, and W. W. Benson, editors. Plant–animal interactions: evolutionary ecology in tropical and temperate regions. Wiley and Sons, New York, New York, USA.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305–335.

Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. Science 230:895–899.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302–1309.

Connell, J. H., and E. Orias. 1964. The ecological regulation of species diversity. American Naturalist 98:399–414.

Conway, T. J., P. P. Tans, L. S. Waterman, and K. W. Thonig. 1994. Evidence for interannual variability of the carbon cycle from the National Oceanic and Atmospheric Administration Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network. Journal of Geophysical Research—Atmospheres 99:22831–22855.

Cotgreave, P. 1993. The relationship between body-size and population abundance in animals. Trends in Ecology and Evolution 8:244–248.

Cousins, S. H. 1989. Species richness and energy theory. Nature 340:350–351.

Cramer, W., D. W. Kicklighter, and A. Bondeau, the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. Global Change Biology 5(Supplement 1):1–15.

Cramer, W., R. J. Olson, S. D. Prince, and J. M. O. Scurlock, and Members of the Global Primary Production Data Initiative. 2001. Determining present patterns of global productivity. Pages 429–448 *in* J. Roy, B. Saugier, and H. A. Mooney, editors. Terrestrial global productivity. Academic Press, San Diego, California, USA.

Currie, D. J., and J. T. Fritz. 1993. Global patterns of animal abundance and species energy use. Oikos 67:56–68.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guegan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134.

Curtis, P. S., P. J. Hanson, P. Bolstad, C. Barford, J. C. Randolph, H. P. Schmid, and K. Wilson. 2002. Allometric and eddy-covariance estimates of annual carbon storage in five eastern North American dcciduous forests. Agricultural and Forest Meteorology 113:3–19.

Damuth, J. 1981. Population density and body size in mammals. Nature 290:699–700.

Damuth, J. 1991. Of size and abundance. Nature 351:268–269.

DeAngelis, D. L., R. H. Gardner, and H. H. Shugart. 1997. NPP multi-biome: global IBP woodlands data, 1955–1975. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. ⟨http://www.daac.ornl.gov/⟩

DeFries, R. S., C. B. Field, I. Fung, G. J. Collatz, and L. Bounoua. 1999. Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. Global Biogeochemical Cycles 13:803–815.

DeFries, R. S., M. C. Hansen, J. R. G. Townshend, A. C. Janetos, and T. R. Loveland. 2000. A new global 1-km dataset of percentage tree cover derived from remote sensing. Global Change Biology 6:247–254.

Denissenko, E. A., V. Brovkin, and W. Cramer. 2001. NPP multi-biome: PIK data for northern Eurasia, 1940–1988. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. ⟨http://www.daac.ornl.gov/⟩

Diniz-Filho, J. A. F. 2008. Bergmann's rule, natural selection and the end of the Panglossian paradigm in ecogeographical analyses. Journal of Biogeography 35:577–578.

Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science 263:185–190.

Dobzhansky, T. 1950. Evolution in the tropics. American Scientist 38:209–221.

Drycz, A. 1985. Breeding ecology of two species of *Turdus grayi* at localities of different human influence in Panama Lowlands. Acta XVIII International Congress of Ornithology. Nauka, Moscow, Russia.

El Saleous, N. Z., E. F Vermote, C. O. Justice, J. R. Townshend, C. J. Tucker, and S. N. Goward. 2000. Improvements in the global biospheric record from the advanced very high resolution radiometer (AVHRR). International Journal of Remote Sensing 21:1251–1277.

Enting, I. G. 2000. Constraints on the atmospheric carbon budget from spatial distributions of CO_2. Pages 115–124 *in* T. M. L. Wigley and D. S. Schimel, editors. The carbon cycle. Cambridge University Press, Cambridge, UK.

Enting, I. G., and J. V. Mansbridge. 1991. Latitudinal distribution of sources and sinks of CO_2: results of an inversion study. Tellus 43B:156–170.

Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopterists Bulletin 36:74–75.

Erwin, T. L. 1983. Beetles and other Arthropods of the tropical forest canopies at Manaus, Brazil, samples with insecticidal fogging techniques. Pages 59–75 *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. Tropical rain forests: ecology and management. Blackwell Scientific Publications, Oxford, UK.

Erwin, T. L. 1988. The tropical forest canopy: the heart of biotic diversity. Pages 123–129 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C., USA.

Erwin, T. L., and J. C. Scott. 1980. Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. Coleopterists Bulletin 34:305–322.

Esser, G. 1998. Multi-biome: global Osnabruck data, 1937–1981. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. ⟨http://www.daac.ornl.gov/⟩

Esser, G., H. F. H. Lieth, J. M. O. Scurlock, and R. J. Olson. 1997. Worldwide estimates and bibliography of net primary productivity derived from pre-1982 publications. ORNL/TM-13485. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Fearnside, P. M. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. Forest Ecology and Management 90:59–87.

Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281: 237–240.

Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the Central Amazonian rainforest ecosystem. Biotropica 5:2–14.

Fleming, I. A., and M. R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology 71:1–11.

Foley, J. A., S. Levis, I. C. Prentice, D. Pollard, and S. T. Thompson. 1998. Coupling dynamic models of climate and vegetation. Global Change Biology 4:561–579.

Food and Agriculture Organization of the United Nations. 2008. Harmonized world soil database v1. 0. FAO/IIASA/ISRIC/JRC-EU/Academia Sinica. FAO Land and Water Digital Media Series #34. Food and Agriculture Organization of the United Nations, Rome, Italy.

Francis, A. P., and D. J. Currie. 1998. Global patterns of species richness in moist forests: another look. Oikos 81:598–602.

Gartlan, J. S., D. B. McKey, P. G. Waterman, C. N. Mbi, and T. T. Struhsaker. 1980. A comparative study of the phytochemistry of two African rainforests. Biochemical Systematics and Ecology 8:401–422.

Gaston, K. J., and T. M. Blackburn. 1996. Global scale macroecology: interactions between population size, geographic range size and body size in Anseriformes. Journal of Animal Ecology 65:701–714.

Gaston, G., S. Brown, M. Lorenzini, and K. D. Singh. 1998. State and change in carbon pools in the forests of tropical Africa. Global Change Biology 4:97–114.

Geist, V. 1987*a*. Bergmann's rule is invalid. Canadian Journal of Zoology 65:1035–1038.

Geist, V. 1987*b*. On speciation in Ice Age mammals, with special reference to cervids and caprids. Canadian Journal of Zoology 65:1067–1084.

Geist, V. 1998. Deer of the world: their evolution, behavior, and ecology. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Geist, V. 1999. Periglacial ecology, large mammals, and their significance to human biology. Pages 78–94 *in* R. Bonnichsen and K. L. Turnmire, editors. Ice age peoples of North America: environments, origins, and adaptations of the first Americans. Oregon State University Press, Corvallis, Oregon, USA.

Glazier, D. S. 1985. Energetics of litter size in five species of *Peromyscus* with generalizations for other mammals. Journal of Mammalogy 66:629–642.

Graves, G. R. 1991. Bergmann's rule near the equator: latitudinal clines in body size of an Andean passerine bird. Proceedings of the National Academy of Sciences (USA) 88: 2322–2325.

Grayson, D. K., and F. Delpech. 2003. Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France). Journal of Archaeological Science 30: 1633–1648.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science 307:550–555.

Greve, M., K. J. Gaston, B. J. van Rensburg, and S. L. Chown. 2008. Environmental factors, regional body size distributions and spatial variation in body size of local avian assemblages. Global Ecology and Biogeography 17:514–523.

Grime, J. P. 1973. Control of species density in herbaceous vegetation. Journal of Environmental Management 1:151–167.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley, New York, New York, USA.

Gross, M. R., R. M. Coleman, and R. M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239:1291–1293.

Guillaumet, A., J.-B. Ferdy, E. Desmarais, B. Godelle, and P.-A. Crochet. 2008. Testing Bergmann's rule in the presence of confounding factors: a case study with three species of Galerida Larks in Morocco. Journal of Biogeography 35: 579–591.

Guthrie, R. D. 1984*a*. Alaskan megabucks, megabulls, and megarams: the issue of Pleistocene gigantism. Pages 482–510 *in* H. H. Genoways and M. R. Dawson, editors. Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.

Guthrie, R. D. 1984*b*. Mosaics, allelochemics, and nutrients: an ecological theory of late Pleistocene megafaunal extinctions. Pages 259–298 *in* P. S. Martin and R. G. Klein, editors. Quaternary extinctions: a prehistoric revolution. University of Arizona Press, Tucson, Arizona, USA.

Hails, C. J. 1982. A comparison of tropical and temperate aerial insect abundance. Biotropica 14:310–313.

Hall, J. B., and M. D. Swaine. 1976. Classification and ecology of closed-canopy forest in Ghana. Journal of Ecology 64: 913–951.

Hamilton, T. H. 1961. The adaptive significances of intraspecific trends in wing length and body size among bird species. Evolution 15:180–195.

Harlow, R. F. 1962. Osteometric data for the Florida black bear. Quarterly Journal of the Florida Academy of Sciences 24:258–274.

Hatcher, P. G., and D. A. Segar. 1976. Chemistry and continental margin sedimentation. Pages 461–477 *in* D. J. Stanley and D. J. P. Swift, editors. Marine sediment transport and environmental management. Wiley and Sons, New York, New York, USA.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guegan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberforff, E. M O'Brien, E. R. Porter, and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Heaney, L. R. 1984. Climatic influences on life-history tactics and behavior of North American tree squirrels. Pages 43–78 *in* J. O. Murie and J. R. Michener, editors. The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, Nebraska, USA.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. American Naturalist 163:192–211.

Hoffman, F. M., C. C. Covey, I. Y. Fung, J. T. Randerson, P. E. Thornton, Y.-H. Lee, N. A. Rosenbloom, R. C. Stöckli, S. W. Running, D. E. Bernholdt, and D. N. Williams. 2007. Results from the carbon–land model intercomparison project (C-LAMP) and availability of the data on the Earth system grid (ESG). Journal of Physics, Conference Series 78:012026.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367–368.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. Tosi. 1971. Forest environments in tropical life zones: a pilot study. Pergamon, New York, New York, USA.

Houghton, R. A., K. T. Lawrence, J. L. Hackler, and S. Brown. 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Global Change Biology 7:731–746.

Houghton, R. A., and D. L. Skole. 1990. Carbon. Pages 393–408 *in* B. L. Turner, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Matthews, and W. B. Meyer, editors. The Earth as transformed by human action. Cambridge University Press, Cambridge, UK.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hussell, D. J. T. 1972. Factors affecting clutch size in Arctic passerines. Ecological Monographs 42:317–364.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Huston, M. A. 1980. Soil nutrients and species richness in Costa Rican forests. Journal of Biogeography 7:147–157.

Huston, M. A. 1993. Biological diversity, soils, and economics. Science 262:1676–80.

Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460.

Huston, M. A. 2005. The three phases of land-use change: implications for biodiversity. Ecological Applications 15: 1864–1878.

Huston, M. A., A. E. Huston, and J. Scurlock. 2000. Shifting the carbon balance. BioScience 50:292.

Hyde, K. J. W., J. E. O'Reilly, and C. A. Oviatt. 2007. Validation of SeaWIFS chlorophyll *a* in Massachusetts Bay. Continental Shelf Research 12:1677–1691.

Imhoff, M. L., L. Bounoua, T. Ricketts, C. Loucks, R. Harriss, and W. T. Lawrence. 2004. Global patterns in human consumption of net primary production. Nature 429:870–873.

IPCC. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

IPCC. 2003. Good practice guidance for land use, land-use change and forestry. Intergovernmental Panel on Climate Change National Greenhouse Gas Inventories Program. Institute for Global Environmental Strategies, Hayama, Kanagawa, Japan.

IPCC. 2007. Climate change 2007: synthesis report. Summary for policymakers. Fourth Assessment Report. Intergovernmental Panel on Climate Change, Gland, Switzerland.

Iriarte, J. A., W. L. Franklin, W. E. Johnson, and K. H. Redford. 1990. Biogeographic variation of food habits and body size of the American puma. Oecologia 85:185–190.

Irigoien, X., J. Huisman, and R. P. Harris. 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. Nature 429:863–867.

Jackson, R. B., J. Canadell, J. R. Ehlringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411.

Jackson, R. B., H. A. Mooney, and E. D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proceedings of the National Academy of Sciences USA 94:7362–7366.

James, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51:365–390.

Johnson, C. N. 1998. Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. Journal of Animal Ecology 67:689–698.

Johnston, R. F. 1954. Variation in breeding season and clutch size in song sparrows of the Pacific coast. Condor 56:268–273.

Jordan, C. F. 1971*a*. A world pattern in plant energetics. American Scientist 59:425–433.

Jordan, C. F. 1971*b*. Productivity of a tropical rain forest and its relation to a world pattern of energy storage. Journal of Ecology 59:127–142.

Karanth, K. U., and M. E. Sunquist. 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarohole, India. Journal of Tropical Ecology 8:21–35.

Keeling, H. C., and O. L. Phillips. 2007. The global relationship between forest productivity and biomass. Global Ecology and Biogeography 16:618–631.

Kennedy, M. L., P. K. Kennedy, M. A. Bogan, and J. L. Waits. 2002. Geographic variation in the black bear (*Ursus americanus*) in the eastern United States and Canada. Southwestern Naturalist 47:257–266.

Kennedy, M. L., and S. L. Lindsay. 1984. Morphologic variation in the raccoon, *Procyon lotor*, and its relationship to genic and environmental variation. Journal of Mammalogy 65:195–205.

Kicklighter, D. W., A. Bondeau, and A. L. Schloss, the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): global pattern and differentiation by major biomes. Global Change Biology 5(Supplement 1):16–24.

Kie, J. G., M. White, and D. L. Drawe. 1983. Condition parameters of white-tailed deer in Texas. Journal of Wildlife Management 47:583–594.

Kilgore, D. L., Jr. 1970. The effects of northward dispersal on growth rate of young, size of young at birth, and litter size in *Sigmodon hispidus*. American Midland Naturalist 84:510–520.

Kleidon, A., and H. A. Mooney. 2000. A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. Global Change Biology 6: 507–523.

Klein, R. G. 1986. Carnivore size and Quaternary climatic change in southern Africa. Quaternary Research 26:153–170.

Klein, D. R., M. Meldgaard, and S. G. Fancy. 1987. Factors determining leg length in *Rangifer tarandus*. Journal of Mammalogy 68:642–655.

Klomp, H. 1970. The determination of clutch size in birds. A review. Ardea 58:1–124.

Koenig, W. D. 1986. Geographical ecology of clutch size variation in North American woodpeckers. Condor 88:499–504.

Körner, C. 2003. Slow in, rapid out: carbon flux studies and Kyoto targets. Science 300:1242–1243.

Korpimäki, E., and J. Wiehn. 1998. Clutch size of Kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. Oikos 83:259–272.

Koss, W. J., J. R. Owenby, P. M. Steurer, and D. S. Ezell. 1988. Freeze/frost data. Climatography of the U.S. No. 20, Supplement 1. National Climate Data Center, National Oceanic and Atmospheric Administration, Asheville, North Carolina, USA.

Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, San Diego, California, USA.

Kurtén, B. 1958. Life and death of the Pleistocene cave bear: a study in paleoecology. Acta Zoologica Fennica 95:4–59.

Kurtén, B. 1963. Fossil bears from Texas. The Pearce-Sellards Series, Texas Memorial Museum 1:1–15.

Kurtén, B. 1973. Geographic variation in size in the puma (*Felis concolor*). Commentationes Biologicae 63:3–8.

Kurtén, B. 1976. The cave bear story: life and death of a vanished animal. Columbia University Press, New York, New York, USA.

Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.

Lack, D. 1947. The significance of clutch size, Part I. Ibis 89: 302–352.

Lack, D. 1948. The significance of clutch size, Part II. Ibis 90: 24–45.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, UK.

Lack, D., and R. E. Moreau. 1965. Clutch size in tropical birds of forest and savanna. Oiseau 35:76–89.

Lagerloef, G., G. T. Mitchum, R. Lukas, and P. Niler. 1999. Tropical Pacific near surface currents estimated from altimeter, wind, and drifter data. Journal of Geophysical Research 104:23,313–23.

Lambers, H., J. A. Raven, G. R. Shaver, and S. E. Smith. 2008. Plant nutrient-acquisition strategies change with soil age. Trends in Ecology and Evolution 23:95–103.

Landahl, J. T., and R. B. Root. 1969. Differences in life tables of tropical and temperate milkweed bugs, genus *Oncopeltus* (Hemiptera: Lygaeidae). Ecology 50:734–737.

Langvatn, R., and S. D. Albon. 1986. Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's Rule. Holarctic Ecology 9:285–293.

Laurance, W. F., M. A. Cochrane, S. Bergen, P. M. Fearnside, P. Delamonica, C. Barber, S. D'Angelo, and T. Fernandes. 2001. The future of the Brazilian Amazon. Science 291:438–439.

Laurance, W. F., P. M. Fearnside, S. G. Laurance, P. Delamonica, T. E. Lovejoy, J. M. Rankin-de-Merona, J. Q. Chambers, and C. Gascon. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. Forest Ecology and Management 118:127–138.

Laws, E. A., P. G. Falkowski, W. O. Smith, Jr., H. Ducklow, and J. J. McCarthy. 2000. Temperature effects on export production in the open ocean. Global Biogeochemical Cycles 14:1231–1246.

Leigh, E. G. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, New York, New York, USA.

Leith, H. 1975. Modeling the primary productivity of the world. Pages 237–263 *in* H. Leith and R. H. Whittaker, editors. Primary productivity of the biosphere. Springer-Verlag, New York, New York, USA.

Leith, H., and R. H. Whittaker, editors. 1975. Primary productivity of the biosphere. Springer-Verlag, New York, New York, USA.

Lima, S. L. 1987. Clutch size in birds: a predation perspective. Ecology 68:1062–1070.

Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. Evolution 20:456–465.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology 67:413–418.

Llach Cordero,, L. 1969. Mechanical and physical properties of 113 (Panamanian) species. Part 3 (Propiedades fisicaz y mecanicas de ciento trece especies, Parte 3). Iforme sobre un programa de ensayo de maderas, Proyecto UNDP 192. FAO/IICA, Turrialba, Costa Rica.

Loehle, C. 1988. Tree life history strategies: the role of defense. Canadian Journal of Forest Research 18:209–222.

Loescher, H. W., B. E. Law, L. Mahrt, D. Y. Hollinger, J. Campbell, and S. C. Wofsy. 2006. Uncertainties in, and interpretation of, carbon flux estimates using the eddy covariance technique. Journal of Geophysical Research 111: D21S90.

Loescher, H. W., S. F. Oberbauer, H. L. Gholz, and D. B. Clark. 2003. Environmental controls on net ecosystem-level carbon exchange and productivity in a Central American tropical wet forest. Global Change Biology 9:396–412.

Lord, R. D., Jr. 1960. Litter size and latitude in North American mammals. American Midland Naturalist 64:488–499.

Maehr, D. S., E. C. Hellgren, R. L. Bingham, and D. L. Doan-Crider. 2001. Body mass of American black bears from Florida and Mexico. Southwestern Naturalist 46:129–133.

Maehr, D. S., and C. T. Moore. 1992. Models of mass growth for 3 North American cougar populations. Journal of Wildlife Management 56:700–707.

Mahli, Y., A. D. Nobre, J. Grace, B. Kruijt, M. G. P. Pereira, A. Culf, and S. Scott. 1998. Carbon dioxide transfer over a Central Amazonian rain forest. Journal of Geophysical Research—Atmospheres 103:31593–31612.

Marcotullio, P. J., and F. B. Gill. 1985. Use of time and space by Chestnut-backed Antbirds. Condor 87:187–191.

Marin, M. 1999. Growth rates in the Black Swift: temperate versus tropical comparisons. Ornithologia Neotropical 10: 179–192.

Marra, J., C. Ho, and C. C. Trees. 2003. An alternative algorithm for the calculation of primary productivity from remote sensing data. LDEO Technical Report LDEO-2003-1. Lamont-Doherty Earth Observatory of Columbia University, New York, New York, USA.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. Science 287:1482–1485.

Matthews, E. 1997. Global litter production, pools, and turnover times: estimates from measurement data and regression models. Journal of Geophysical Research 102(D15): 18771–18800.

McArthur, W. M. 1991. Reference Soils of south-western Australia. Department of Agriculture, Perth, Australia.

McKenzie, N. J., D. Jacquier, R. F. Isbell, and K Brown. 2004. Australian soils and landscapes: an illustrated compendium. CSIRO Publishing, Melbourne, Australia.

McKey, D. 1974. Adaptive patterns in alkaloid physiology. American Naturalist 108:305–320.

McKey, D. 1980. The evolution of novel alkaloid types: a mechanism for the rapid phenotypic evolution of plant secondary compounds. American Naturalist 115:754–759.

McKey, D. B., P. G. Waterman, C. N. Mbi, J. S. Gartlan, and T. T. Struhsaker. 1978. Phenolic content of vegetation in two African rain-forests: ecological implications. Science 202:61–64.

Meentemeyer, V. 1978*a*. Climatic regulation of decomposition rates of organic matter in terrestrial systems. Pages 779–789 *in* D. C. Adriano and I. L. Brisbin, editors. Environmental chemistry and cycling processes. CONF 760429. National Technical Information Service, Springfield, Virginia, USA.

Meentemeyer, V. 1978*b*. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472.

Meggers, B. J. 1971. Amazonia: man and culture in a counterfeit paradise. Aldine-Atherton, Chicago, Illinois, USA.

Meiri, S., T. Dayan, and D. Simberloff. 2004. Carnivores, biases and Bergmann's rule. Biological Journal of the Linnean Society 81:579–588.

Meiri, S., Y. Yom-Tov, and E. Geffen. 2007. What determines conformity to Bergmann's Rule? Global Ecology and Biogeography 16:788–794.

Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626.

Mikola, P. 1962. Temperature and tree growth near the northern tree line. Pages 265–274 *in* T. Kozlowski, editor. Tree growth. Ronald Press, New York, New York, USA.

Millar, J. S. 1978. Energetics of reproduction in *Peromyscus leucopus*: the cost of lactation. Ecology 59:1055–1061.

Minami, H., and H. Ogi. 1997. Determination of migratory dynamics of the sooty shearwater in the Pacific using stable carbon and nitrogen isotope analysis. Marine Ecology Progress Series 158:249–256.

Mitchell, H. L. 1965. Highlights of results of the Southern wood density survey. Pages 38–64 *in* Proceedings of the symposium on density: a key to wood quality. U.S. Forest Service, Forest Products Laboratory, Madison, Wisconsin, USA.

Mittelbach, G., et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. Ecology Letters 10:315–331.

Murie, J. O., D. A. Boag, and V. K. Kivett. 1980. Litter size in Columbian ground squirrels (*Spermophilus columbianus*). Journal of Mammalogy 61:237–244.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423(6937):280–283.

Myneni, R. B., J. Dong, C. J. Tucker, R. K. Kaufmann, P. E. Kauppi, J. Liski, L. Zhou, V. Alexeyev, and M. K. Hughes. 2001. A large carbon sink in the woody biomass of northern forests. Proceedings of the National Academy of Sciences (USA) 98:147840–14789.

Nadelhoffer, K. J., J. W. Raich, and J. D. Aber. 1998. A global trend in belowground carbon allocation: comment. Ecology 79:1822–1825.

New, M., M. Hulme, and P. D. Jones. 1999. Representing twentieth century space-time climate variability. Part I. Development of a 1961–1990 mean monthly terrestrial climatology. Journal of Climate 12:829–856.

New, M., M. Hulme, and P. D. Jones. 2000. Representing twentieth century space-time climate variability. Part II. Development of a 1961–1990 mean monthly terrestrial climate fields. Journal of Climate 13:2217–2238.

Ni, J., X. S. Zhang, and J. M. O. Scurlock. 2001. NPP multi-biome: Chinese forests data, 1989–1994. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. ⟨http://www.daac.ornl.gov/⟩

Nowak, R. M., and J. L. Paradiso. 1983. Walker's mammals of the world. Johns Hopkins University Press, Baltimore, Maryland, USA.

Olson, R. J., K. R. Johnson, D. L. Zheng, and J. M. O. Scurlock. 2001*a*. Global and regional ecosystem modeling: databases of model drivers and validation measurements. ORNL/TM-2001/196. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Olson, R. J., J. M. O. Scurlock, S. D. Prince, D. L. Zhang, , and K. R. Johnson, editors. 2001*b*. NPP multi-biome: global primary production data initiative products. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. ⟨http://www.daac.ornl.gov/⟩

Olson, J. S., J. S. Watts, and L. J. Allison. 1983. Carbon in live vegetation of major world ecosystems. Publication ORNL-5882. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

O'Neill, R. V., and D. L. DeAngelis. 1981. Comparative productivity and biomass relations of forest ecosystems. Pages 411–449 *in* D. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, UK.

Open University Course Team. 2001. Ocean circulation. Butterworth-Heinemann, Oxford, UK.

O'Reilly, J. E., S. Maritorena, B. G. Mitchell, D. A. Siegel, K. L. Carder, S. A. Garver, M. Kahru, and C. R. McClain.

1998. Ocean color algorithms for SeaWIFS. Journal of Geophysical Research 103:24937–24953.

Owen-Smith, R. N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge, UK.

Parsons, R. F. 1967. Effect of age on root:shoot ratios in some herbaceous and woody plants: an appraisal. Bulletin of the Torrey Botanical Club 94:498–500.

Patrick, R., and D. Strawbridge. 1963. Variation in the structure of natural diatom communities. American Naturalist 97:51–57.

Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature 374:255–257.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. Science 279: 860–863.

Payne, R. B. 1976. The clutch size and number of eggs of Brown-headed Cowbirds: effects of latitude and breeding season. Condor 78:337–342.

Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. Journal of Animal Ecology 34: 601–647.

Peschen, D. P. 1972. *Chrysolina quadrigemina* (Coleoptera: Chrysomelidae) introduced from California to British Columbia against the weed *Hypericum perforatum*: comparison of behaviour, physiology, and colour in association with post-colonization adaptation. Canadian Entomology 104: 1689–1698.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, New York, New York, USA.

Petrides, G. A., and W. G. Swank. 1965. Population densities and the range-carrying capacity for large mammals in Queen Elizabeth National Park, Uganda. Zoologia Africana 1:209–225.

Petrides, G. A., and W. G. Swank. 1966. Estimating the productivity and energy relations of an African Elephant population. Proceedings of the International Grassland Conference, Sao Paulo, Brazil 9:831–942.

Phillips, O. L., et al. 2004. Pattern and process in Amazon tree turnover, 1976–2001. Philosophical Transactions of the Royal Society London, Series B 359:381–407.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. American Naturalist 100:33–46.

Post, W. M., W. R. Emmanuel, P. J. Zinke, and A. G. Stangenberger. 1982. Soil carbon pools and world life zones. Nature 298:156–159.

Post, W. M., J. Pastor, P. J. Zinke, and A. G. Stangenberger. 1985. Global patterns of soil nitrogen storage. Nature 317: 613–616.

Potter, C. S. 1999. Terrestrial biomass and the effects of deforestation on the global carbon cycle. BioScience 49:769–778.

Potter, C. S., J. T. Randerson, C. B. Field, P. A. Matson, P. M. Vitousek, H. A. Mooney, and S. A. Klooster. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochemical Cycles 7:811–841.

Poulin, R. 1995. Clutch size and egg size in free-living and parasitic copepods: a comparative analysis. Evolution 49: 325–336.

Poulin, R., and W. J. Hamilton. 1995. Ecological determinants of body size and clutch size in amphipods: a comparative approach. Functional Ecology 9:364–370.

Pregitzer, K. S., and E. S. Euskirchen. 2004. Carbon cycling and storage in world forests: biome pattern related to forest age. Global Change Biology 10:2052–2077.

Price, P. W. 1974. Strategies for egg production. Evolution 28: 76–84.

Proctor, J. 1983. Tropical forest litter: I. Problems of data comparison. Pages 267–273 *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. Tropical rain forest: ecology and management. Blackwell, Oxford, UK.

Radtke, M. G., C. R. V. da Fonseca, and G. B. Williamson. 2007. Dung beetle biomass, abundance, and species diversity. Biotropica 39:725–730.

Raich, J. W., and K. J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70: 1346–1354.

Rassweiler, A., K. K. Arkema, D. C. Reed, R. C. Zimmerman, and M. A. Brzezinski. 2008. Net primary production, growth, and standing crop of *Macrocystis pyrifera* in southern California. Ecology 89:2068.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. American Scientist 46:205–221.

Redfield, A. C., B. H. Ketchum, and R. A. Richards. 1963. The influence of organisms on the composition of sea water. Pages 26–77 *in* M. N. Hill, editor. The sea. Volume 2. Wiley, New York, New York, USA.

Richardson, T. L., and G. A. Jackson. 2007. Small phytoplankton and carbon export from the surface ocean. Science 315:838–840.

Richter, D. D., and L. I. Babbar. 1991. Soil diversity in the tropics. Advances in Ecological Research 21:316–389.

Ricklefs, R. E. 1970. Clutch size in birds: outcome of opposing predator and prey adaptations. Science 168:599–600.

Ricklefs, R. E. 1976. Growth rates of birds in the humid New World tropics. Ibis 118:179–207.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38–49.

Ricklefs, R. E. 1983. Avian postnatal development. Pages 1–83 *in* D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian biology. Volume 7. Academic Press, New York, New York, USA.

Ritke, M. E., and M. L. Kennedy. 1988. Intraspecific morphologic variation in the raccoon (*Procyon lotor*) and its relationship to selected environmental variables. Southwestern Naturalist 33:295–314.

Rodríguez, M. Á., I. L. López-Sañudo, and B. A. Hawkins. 2006. The geographic distribution of mammal body size in Europe. Global Ecology and Biogeography 15:173–181.

Rodríguez-Iturbe, I., and A. Rinaldi. 1997. Fractal river basins, chance and self-organization. Cambridge University Press, New York, New York, USA.

Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population dynamics of black bears in northeastern Minnesota. Wildlife Monographs 97.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527.

Rosenzweig, M. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171: 385–387.

Rosenzweig, M. 1995. Species diversity in time and space. Cambridge University Press, Cambridge, UK.

Rotenberry, J. T., and J. A. Wiens. 1989. Reproductive biology of shrub-steppe passerine birds: geographical and temporal variation in clutch size, brood size, and fledging success. Condor 91:1–14.

Roy, J., B. Saugier, and H. A. Mooney, editors. 2001. Terrestrial global productivity: past, present, and future. Academic Press, San Diego, California, USA.

Ruimy, A., L. Kergoat, and A. Bondeau, the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. Global Change Biology 5(Supplement 1):56–64.

Running, S. W., D. D. Baldocchi, D. P. Turner, S. T. Gower, P. S. Bawkin, and K. A. Hibbard. 1999. A global terrestrial monitoring network, scaling tower fluxes with ecosystem modeling and EOS satellite data. Remote Sensing of the Environment 70:108–127.

Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto. 2004. A continuous satellite-derived measure of global primary production. BioScience 54:547–560.

Russell, E. W. B. 1997. People and the land through time: linking ecology and history. Yale University Press, New Haven, Connecticut, USA.

Saleska, S. R., et al. 2003. Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. Science 302:1554–1557.

Sanchez, P. A. 1976. Properties and management of soils in the tropics. John Wiley and Sons, New York, New York, USA.

Sanz, J. J. 1997. Geographic variation in breeding parameters of the Pied Flycatcher (*Ficedula hypoleuca*). Ibis 139:107–114.

Sanz, J. J. 1998. Effects of geographic location and habitat on breeding parameters of Great Tits. Auk 115:1034–1051.

Sarmiento, J. L., N. Gruber, M. A. Brzezinski, and J. P. Dunne. 2004. High-latitude controls of thermocline nutrients and low latitude biological productivity. Nature 427:56–60.

Saugier, B., J. Roy, and H. A Mooney. 2001. Estimations of global terrestrial productivity: converging toward a single number? Pages 543–557 *in* J. Roy, B. Saugier, and H. A. Mooney, editors. Terrestrial global productivity. Academic Press, San Diego, California, USA.

Schloss, A. L., D. W. Kicklighter, and J. Kaduk, the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): comparison of NPP to climate and the normalized difference vegetation index (NDVI). Global Change Biology 5(Supplement 1):25–34.

Scurlock, J. M. O., W. Cramer, R. H. Olson, W. J. Parton, and S. D. Prince. 1999. Terrestrial NPP: toward a consistent data set for global model evaluation. Ecological Applications 9: 913–919.

Scurlock, J. M. O., K. Johnson, and R. J. Olson. 2002. Estimating net primary productivity from grassland biomass dynamics measurements. Global Change Biology 8:736–753.

Scurlock, J. M. O., and R. J. Olson. 2002. Terrestrial net primary productivity: a brief history and new worldwide database. Environmental Reviews (NRC-CNRC) 10:91–110.

Seagle, S. W., and B. R. Sturtevant. 2005. Forest productivity predicts invertebrate biomass and Ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian forests. Ecology 86: 1531–1539.

Siegel, D. A., S. C. Doney, and J. A. Yoder. 2002. The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. Science 296:730–733.

Silver, S. C., L. E. T. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gómez, and G. Ayala. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38:148–154.

Simard, M. A., S. D. Côté, R. B. Weladji, and J. Huot. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. Journal of Animal Ecology 77:678–686.

Simonstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. Science 200:403–411.

Sinclair, A. R. E., and P. Arcese. 1995. Serengeti II dynamics, management, and conservation of an ecosystem. The University of Chicago Press, Chicago, Illinois, USA.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds. Ornithological Monographs 36: 575–594.

Smith, M. H., and J. T. McGinnis. 1968. Relationships of latitude, altitude, and body size to litter size and mean annual production of offspring in *Peromyscus*. Researches on Population Ecology 10:115–126.

Smith, W. O., and D. J. Demaster. 1996. Phytoplankton biomass and productivity in the Amazon river plume: correlation with seasonal river discharge. Continental Shelf Research 16:291–319.

Snow, D. W. 1958. The breeding of the Blackbird, *Turdus merula*, at Oxford. Ibis 100:1–30.

Spear, L. B., and D. G. Ainley. 1999. Migration routes of sooty shearwaters in the Pacific Ocean. Condor 101:205–218.

Spencer, A. W., and H. W. Steinhoff. 1968. An explanation of geographic variation in litter size. Journal of Mammalogy 49: 281–286.

Stenseth, N. C., T. O. Gustafsson, L. Hansson, and K. I. Ugland. 1985. On the evolution of reproductive rates in microtine rodents. Ecology 66:1795–1808.

Stevick, P. T., B. J. McConnell, and P. S. Hammond. 2002. Patterns of movement. Pages 185–216 *in* A. R. Hoelzel, editor. Marine mammal biology: an evolutionary approach. Blackwell, New York, New York, USA.

Stiner, M. C. 1998. Mortality analysis of Pleistocene cave bears and its paleoanthropological relevance. Journal of Human Evolution 34:303–326.

Strakhov, N. M. 1967. Principles of lithogenesis. Volume 1. Oliver and Boyd, Edinburgh, UK.

Talbot, L. M., and M. H. Talbot. 1963. The high biomass of wild ungulates on East African Savanna. Transactions of the North American Wildlife Conference 28:465–476.

Teer, J. G., J. W. Thomas, and E. A. Walker. 1965. Ecology and management of white-tailed deer in the Llano Basin of Texas. Wildlife Monographs 15.

Terborgh, J. L., H. Emmons, and C. Freese. 1986. La fauna silvestre de la Amazonia: el dispilfarro de un recurso de un renovable. Boletin Lima 46:77–85.

Ter-Mikaelian, M. T., and M. D. Korzukhin. 1997. Biomass equations for sixty-five North American tree species. Forest Ecology and Management 97:1–24.

Thiollay, J.-M. 1988. Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. Oikos 53:17–30.

Toggweiler, J. R., K. Dixon, and W. S. Broecker. 1991. The Peru upwelling and the ventilation of the South Pacific thermocline. Journal of Geophysical Research 96:20467–20497.

Tritton, L. M., and J. W Hornbeck. 1982. Biomass equations for major tree species of the northeast. USDA Forest Service General Technical Report NE-69. U.S. Department of Agriculture Forest Service, Northeastern Forest Experimental Station, Broomall, Pennsylvania, USA.

Trujillo, A. P., and H. V. Thurman. 2005. Essentials of oceanography. Eighth edition. Pearson/Prentice Hall, Englewood Cliffs, New Jersey, USA.

Uehara, G., and G. Gillman. 1981. The mineralogy, chemistry, and physics of tropical soils with variable charge clays. Westview Press, Boulder, Colorado, USA.

Valavanis, V. D., A. Kapantagakis, I. Katara, and A. Palialexis. 2004. Critical regions: a GIS-based model of marine productivity hotspots. Aquatic Sciences 66:139–148.

Van Andel, Tjeerd H. 1994. New views on an old planet: a history of global change. Second edition. Cambridge University Press, Cambridge, UK.

Vaughan, D. G. 2006. Recent trends in melting conditions on the Antarctic Peninsula and their implications for ice-sheet mass balance and sea level. Arctic, Alpine, and Antarctic Research 38:147–152.

VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project (VEMAP): comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem response to climate change and CO_2 doubling. Global Biogeochemical Cycles 9:401–437.

Virgós, E., S. Cabezas-Díaz, and J. A. Blanco-Aguiar. 2006. Evolution of life history traits in Leporidae: a test of nest predation and seasonality hypotheses. Biological Journal of the Linnean Society 88:603–610.

Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285–298.

Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry 13:887–115.

Vogt, K. A., C. C. Grier, and D. J. Vogt. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Advances in Ecolological Research 15:303–377.

Vogt, K. A., D. J. Vogt, and J. Bloomfield. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant and Soil 200:71–89.

Vogt, K. A., D. J. Vogt, P. A. Palmiotto, P. Boon, J. O'Hara, and H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil 187:159–219.

Walbridge, M. R., and P. M. Vitousek. 1987. Phosphorus mineralization potentials in acid organic soils: processes affecting $^{32}PO_4^{3-}$ isotope dilution measurements. Soil Biology and Biochemistry 19:709–717.

Walgren, H. E. 1965. Forest Service western woods density survey: phases II (increment core processing) and III (estimating tree specific gravity). Pages 21–35 *in* Proceedings of the symposium on density: a key to wood quality. U.S. Forest Service, Forest Products Laboratory, Madison, Wisconsin, USA.

Walker, T. W., and A. F. R. Adams. 1958. Studies on soil organic matter. I. Influence of phosphorus content of parent materials on accumulation of carbon, nitrogen, sulfur, and organic phosphorus in grassland soils. Soil Science 85:307–318.

Walter, H. 1973. Die Vegetation der Erde, Bd. II: Tropische und subtropische Zonen. 3. Fischer, Jena-Stuttgart, Germany.

Walter, H. 2002. Vegetation of the Earth. Fourth English edition. Springer-Verlag, Berlin, Germany.

Walter, H., and H. H. Leith. 1967. Klimadiagramm-Weltatlas. VEB Gustav Fischer, Jena, Switzerland.

Waterman, P. G., C. N. Mbi, D. McKey, and J. S. Gartlan. 1980. African rainforest vegetation and rumen microbes: phenolic compounds and nutrients as correlates of digestibility. Oecologia 47:22–33.

WBGU (Wissenschaftlicher Beirat der Bundesregierung Globale Umweltveränerungen). 1988. Die Anrechnung biolischer Quellen und Senken in Kyoto-Protokoll: Fortschritt oder Rückschlang für den globalen Umweltschutz Sondergutachten 1988. Bremerhaven, Germany.

Westlake, D. F. 1963. Comparisons of plant productivity. Biological Review 38:385–425.

White, E. P., S. K. Morgan Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in Ecology and Evolution 22:323–330.

Whitmore, T. C. 1984. Tropical rain forests of the far east. Second edition. Oxford University Press, New York, New York, USA.

Whitney, G. G. 1995. From coastal wilderness to fruited plain: a history of environmental change in temperate North America from 1500 to the present. Cambridge University Press, Cambridge, UK.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Wolverton, S. 2006. Natural-trap ursid mortality and the Kurtén response. Journal of Human Evolution 50:540–551.

Wolverton, S. 2008. Characteristics of late Holocene black bears in Missouri: evidence from two natural traps. Ursus 19: 177–184.

Wolverton, S., M. A. Huston, J. H. Kennedy, K. E. Cagle, and J. D. Cornelius. *In press*. Conformation to Bergmann's Rule in white-tailed deer can be explained by food availability. American Midland Naturalist.

Wolverton, S., J. H. Kennedy, and J. D. Cornelius. 2007. A paleozoological perspective on white-tailed deer (*Odocoileus virginianus texana*) population density and body size in central Texas. Environmental Management 39:545–552.

Wolverton, S., and R. L. Lyman. 1998. Measuring late Quaternary ursid diminution in the Midwest. Quaternary Research 49:322–329.

Wooller, R. D., D. A. Saunders, J. S. Bradley, and C. P. deRebeira. 1985. Geographical variation in size of an Australian honeyeater (Aves: Meliphagidae): an example of Bergmann's rule. Biolgical Journal of the Linnean Society 25: 355–363.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. Oikos 41:495–506.

Yanchuck, A. D., B. P. Dancik, and M. M. Micko. 1983. Intraclonal variation in wood density of trembling aspen in Alberta. Wood Fiber Science 15:387–394.

Yom-Tov, Y., M. I. Christie, and G. J. Iglesias. 1994. Clutch size in passerines of southern South America. Condor 96: 170–177.

Young, B. E. 1994. Geographic and seasonal patterns of clutch size variation in House Wrens. Auk 111:545–555.

Zinke, P. J., A. G. Stangenberger, W. M. Post, W. R. Emanuel, and J. S. Olson. 1984. Worldwide organic soil carbon and nitrogen data. ORNL/TM-8857. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

SUPPLEMENT 1

Basal area and ancillary data for forest sites around the world (*Ecological Archives* M079-012-S1).

SUPPLEMENT 2

NPP, biomass, and ancillary data for forest sites around the world (*Ecological Archives* M079-012-S2).