Patterns of new versus recycled primary production in the terrestrial biosphere

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Edited by Pamela A. Matson, Stanford University, Stanford, CA, and approved June 17, 2013 (received for review February 13, 2013)

Nitrogen (N) and phosphorus (P) availability regulate plant productivity throughout the terrestrial biosphere, influencing the patterns and magnitude of net primary production (NPP) by land plants both now and into the future. These nutrients enter ecosystems via geologic and atmospheric pathways and are recycled to varying degrees through the plant–soil–microbe system via organic matter decay processes. However, the proportion of global NPP that can be attributed to new nutrient inputs versus recycled nutrients is unresolved, as are the large-scale patterns of variation across terrestrial ecosystems. Here, we combined satellite imagery, biogeochemical modeling, and empirical observations to identify previously unrecognized patterns of new versus recycled nutrient (N and P) productivity on land. Our analysis points to tropical forests as a hotspot of new NPP fueled by new N (accounting for 45% of total new NPP globally), much higher than previous estimates from temperate and high-latitude regions. The large fraction of tropical forest NPP resulting from new N is driven by the high capacity for N fixation, although this varies considerably within this diverse biome; N deposition explains a much smaller proportion of new NPP. By contrast, the contribution of new N to primary productivity is lower outside the tropics, and worldwide, new P inputs are uniformly low relative to plant demands. These results imply that new N inputs have the greatest capacity to fuel additional NPP by terrestrial plants, whereas low P availability may ultimately constrain NPP across much of the terrestrial biosphere.

carbon cycle | nutrient cycling | stoichiometry

Rates of net primary productivity (NPP) vary widely across the terrestrial biosphere, with tropical forests accounting for more than one-third of total global annual NPP, and nearly 40% of NPP in natural ecosystems (1, 2). At the global scale, latitudinal variations in climate help explain broad patterns of NPP observed across the land surface, and ample rainfall and sunlight, warm temperatures, and long growing seasons near the equator fuel high rates of NPP in tropical forests (1). Mineral nutrients—especially nitrogen (N) and phosphorus (P)—also influence the patterns and magnitude of NPP, mainly via strong regulatory effects on plant growth and photosynthesis (3). Multiple lines of evidence suggest that N, P, or N + P colimitation are nearly ubiquitous in the terrestrial biosphere (4–8), yet the extent to which nutrient availability might constrain future plant productivity—an important pathway toward higher net global C storage—remains contentious but potentially profound (9–11). For example, model forecasts that consider nutrient limitations of NPP suggest modest (0.18–0.3 °C) to up to 3 °C of additional warming by 2100 compared with carbon–climate simulations (12, 13). These differences hinge largely on N fixation responses to elevated CO_2 and climate (12).

In the 1970s, the widely recognized importance of new nutrient inputs in sustaining algal productivity, ecosystem functioning, and organic matter fluxes through the thermocline in the oceans (i.e., the biological pump) gave rise to the concept of new versus recycled production (14). Model-based applications of this concept identified major regions of the ocean where nutrient inputs via rivers, upwelling, or from external atmospheric sources replenish phytoplankton productivity (15). Areas of relatively high new production were thereby identified as more capable of sustaining resource extractions relative to areas of low new production, particularly fish harvest at higher trophic levels. High new production also tends to fuel organic C storage in the marine biosphere (14). On land, such large-scale patterns of nutrient use have not been defined or systematically investigated, although empirical evidence from a handful of sites in temperate regions suggests that recycled nutrients account for the overwhelming majority of NPP (∼95%) (16–18). However, some analyses indicate that new nutrient inputs via atmospheric deposition (19, 20) and/or N fixation (21–23) can be substantial in some ecosystems, leading to questions about the role of new versus recycled nutrients in sustaining terrestrial productivity across the terrestrial biosphere both now and into the future. Mass balance constraints dictate that long-term C gains in nutrient-limited ecosystems can only be achieved where nutrient inputs are substantial enough to offset nutrient losses from land ecosystems (6, 24, 25).

Here, we combine space-borne satellite data, biogeochemical modeling, and empirical observations to identify current patterns of nutrient cycling and rates of new versus recycled production across a range of natural (i.e., nonagricultural) terrestrial ecosystems. Our approach is based on a simple mass-balance principle: that nutrient uptake can be estimated from plant nutrient demand, calculated as the product of plant-part-specific annual production values (i.e., C allocated in leaves, roots, and shoots) and corresponding plant-part-specific C:N and C:P stoichiometry (Methods and *SI Methods*). Field-based nutrient input and mineralization rate estimates vary considerably in both space and time, are challenged by many methodological limitations, and are difficult to scale up, substantially reducing the efficacy of using plot-level measurements of nutrient cycling and mineralization fluxes to estimate actual plant demand or uptake. However, using satellite-based estimates of NPP and empirical estimates of plant stoichiometry allowed us to examine large-scale patterns in nutrient demand and cycling and to assess spatial variability in new versus recycled productivity across the globe.

Results and Discussion

At the global scale, our analysis points to highly efficient rates of nutrient recycling in natural terrestrial ecosystems (Fig. 1).

Author contributions: C.C.C., B.Z.H., S.C.R., W.P., and S.W.R. designed research; C.C.C., B.Z.H., W.K.S., A.R.M., and S.J.D.G. performed research; W.K.S. and A.R.M. analyzed data; and C.C.C., B.Z.H., W.K.S., A.R.M., S.C.R., W.P., S.J.D.G., and S.W.R. wrote the paper.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1302768110/-/DCSupplemental.

Globally, recycled N accounts for nearly 90% of annual terrestrial plant demand, whereas recycled P sustains >98% of global terrestrial plant productivity (Tables 1 and 2). These numbers are especially significant when considered in light of human cropping systems where <50% of annual fertilized crop N demand is met via recycling (26). This highly efficient nutrient recycling via plant–soil–microbe interactions represents a vital global ecosystem service.

Across the land surface and even within biomes, the quantity of new versus recycled production varies dramatically. For instance, new N inputs have the capacity to support roughly 30% of total annual NPP in savanna ecosystems, but variability within this biome is high, ranging from 3–54% of production at a 10-km^2 spatial resolution (Table 3). This likely reflects the relatively open N cycle in savannas, where fire and herbivory remove N and promote high rates of N fixation, thus limiting the capacity for nutrient recycling. In addition, using our combined satellite and modeling approach, we identify a strong latitudinal difference in new versus recycled production via N (Fig. 1). For example, in boreal and temperate regions (evergreen needeleaf forest) new N production is low (~3%), whereas in tropical forest ecosystems that dominate the

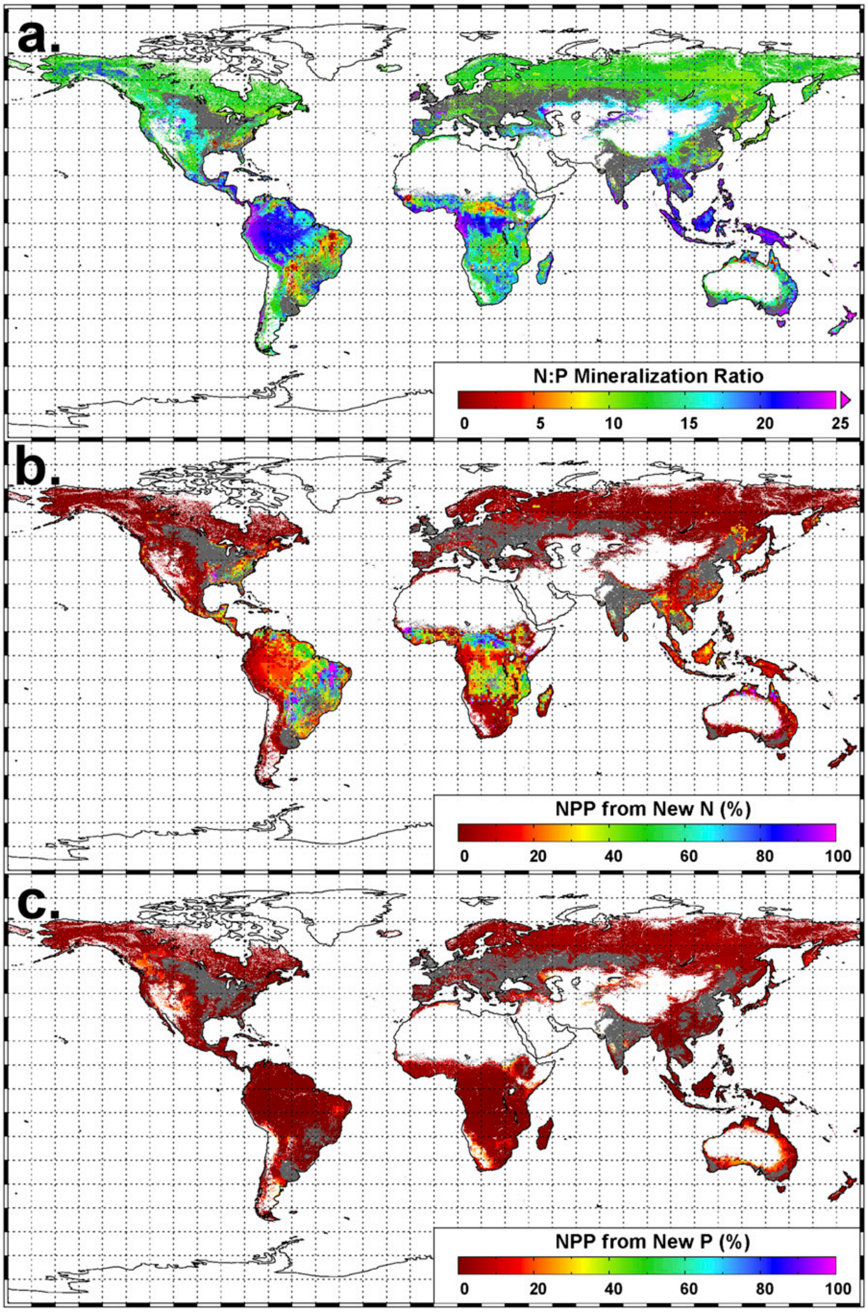

Fig. 1. Global patterns of nitrogen:phosphorus (N:P) mineralization (*A*), NPP from new N (*B*), and NPP from new P (*C*). We excluded agricultural lands from the analysis (gray), and low-productivity regions (i.e., NPP <150 g $C \cdot m^{-2} \cdot y^{-1}$) were masked from the figure (white) because of their extremely low nutrient demands. Nutrient mineralization ratios and new versus recycled production percentages for both N and P were estimated using a combination of satellite-derived NPP data, biogeochemical modeling, and empirical observations (*SI Methods*). Evergreen broadleaf tropical forests account for ~45% of total NPP derived from new N inputs (Table 3).

Table 1. New and recycled N inputs and total N demand by biome

	New N inputs, Tg·y^{-1}, %					Recycled N, Tg·y^{-1}, %		
	N fixation							
Biome	Symbiotic	Asymbiotic	N deposition	Total new N	N resorption	N mineralization	Total recycled N	Total N demand, Tg·y^{-1}
ENF	0.3 (1%)	0.5 (1%)	0.2 (<1%)	1.0 (2%)	11.9 (30%)	26.9 (68%)	39.0 (98%)	39.7
EBF	38.0 (7%)	11.2 (2%)	1.0 (<1%)	50.1 (9%)	167.2 (31%)	323.2 (60%)	491.4 (91%)	540.6
DNF	<0.1 (<1%)	0.1 (1%)	<0.1 (<1%)	0.2 (2%)	2.5 (32%)	5.3 (66%)	7.8 (98%)	8.0
DBF	2.2 (11%)	0.3 (1%)	0.2 (<1%)	2.7 (13%)	7.9 (39%)	9.5 (47%)	17.6 (88%)	20.1
MIX	2.1 (3%)	1.2 (2%)	0.9 (1%)	4.2 (5%)	32.4 (41%)	43.2 (54%)	76.5 (96%)	79.8
SHB	3.5 (3%)	3.9 (4%)	0.7 (1%)	8.0 (7%)	30.4 (27%)	73.4 (66%)	104.5 (93%)	111.8
WSV	23.7 (15%)	1.6 (1%)	0.7 (<1%)	26.0 (17%)	46.9 (30%)	82.0 (53%)	129.6 (84%)	154.9
SVN	31.5 (17%)	2.5 (1%)	0.7 (<1%)	34.7 (19%)	52.6 (29%)	94.5 (52%)	147.7 (81%)	181.7
GRS	4.0 (7%)	1.1 (2%)	0.6 (1%)	5.7 (9%)	19.3 (32%)	35.5 (59%)	55.5 (92%)	60.6
Total	105.1 (9%)	22.4 (2%)	5.0 (<1%)	132.5 (11%)	371.1 (31%)	693.6 (58%)	1,069.6 (89%)	1,197.1

Values in parentheses represent the percent of total N demand (final column) met by each process (columns 2–8). DBF, deciduous broadleaf forest; DNF, deciduous needleleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRS, grassland; MIX, mixed forest; SHB, closed shrublands; SVN, savannas; and WSV, woody savannas.

evergreen broadleaf forest biome, new N inputs account for ~18% of current NPP (Table 3), largely reflecting higher rates of N fixation in tropical relative to temperate ecosystems (12, 21). Although difficult to compare with field studies owing to a paucity of data, one analysis suggests that new N production could account for ~4% of plant N demand in a temperate forest at Hubbard Brook in the northeastern United States (17), a number that is generally consistent with our average result (6%) for the mixed forest biome (Table 3).

N fixation accounts for the majority of new N inputs globally (96%), whereas N deposition plays a relatively minor role (4%; Table 1, *SI Methods*, sections S1–S4, and Fig. S1). Thus, although N deposition rates have been increasing in recent decades and are projected to increase (19), they still account for a small proportion of annual nutrient demand globally (<1%), at least relative to biological N fixation (>10%; Table 1, *SI Methods*, and Figs. S1 and S2). For example, we assumed that 15% of N deposition is plant-available (27) (*SI Methods*, sections S1–S4), but even assuming that 100% is biologically available, N deposition would still only account for 3% of global nutrient demand, or 21% of new NPP (*SI Methods*, section S4 and Figs. S1 and S2). Some recent evidence also suggests potentially high N inputs via rock weathering in some areas; including this source would further increase the potential for new N production, although more so at higher latitudes in forests underlain by sedimentary rocks (28).

For P, new inputs via atmospheric deposition are uniformly low across the terrestrial biosphere. New P inputs via weathering of soil minerals are more important (Figs. S3 and S4), but together, new P inputs via both weathering and atmospheric deposition are still very small relative to plant demand. This suggests that P availability may broadly constrain future NPP, especially in ecosystems where N is plentiful. In contrast to N, the P cycle is replenished slowly through geological processes such as tectonics, volcanism, and rock weathering; hence, recycling dominates P-driven patterns of NPP both regionally and globally (Table 2). In fact, accounting for N and P together, roughly 90% of current global NPP is met via nutrient recycling through plants, soils, and microorganisms (Tables 1 and 2), a number that is remarkably similar to values obtained using empirical approaches in ecosystems from which data are available (16–18). Nutrient resorption represents an important pathway of nutrient recycling in all ecosystems (Figs. S2 and S4), with nutrient uptake before leaf fall accounting for 31% of plant N and 40% of plant P demands globally. However, N and P resorption rates also vary across biomes; the relative contributions of P resorption to total nutrient demand are highest in the evergreen broadleaf forests (tropical forests). This likely reflects the low soil available P status of many tropical forests that grow predominantly on highly weathered, relatively P-poor soils (Table 2) and is consistent with observed increases in N:P resorption ratios with increasing latitude (29).

The spatial variation in new NPP from P is also much lower than for N (Fig. 1 and Tables 1 and 2). This leads us to posit that low P has led organisms to develop various mechanisms to cope with low P inputs, including investment in mycorrhizae to acquire mineral P (30), phosphatase production to mineralize organic P (31), and highly responsive P resorption by plants before leaf fall (29). The

Table 2. New and recycled P inputs and total P demand by biome

Biome	P weathering	P deposition	Total new P	P resorption	P mineralization	Total recycled P	P demand
ENF	0.07 (2%)	0.004 (<1%)	0.073 (2%)	1.6 (42%)	2.1 (56%)	3.6 (98%)	3.7
EBF	0.09 (<1%)	0.041 (<1%)	0.126 (<1%)	14.1 (48%)	15.2 (52%)	29.3 (99%)	29.4
DNF	0.02 (2%)	0.001 (<1%)	0.018 (2%)	0.3 (35%)	0.5 (63%)	0.8 (98%)	0.8
DBF	0.01 (1%)	0.001 (<1%)	0.013 (1%)	0.5 (37%)	0.8 (61%)	1.3 (99%)	1.3
MIX	0.07 (1%)	0.015 (<1%)	0.086 (1%)	3.3 (45%)	4.0 (54%)	7.3 (99%)	7.4
SHB	0.55 (6%)	0.085 (1%)	0.633 (6%)	3.3 (33%)	6.0 (60%)	9.3 (94%)	9.9
WSV	0.07 (1%)	0.032 (<1%)	0.104 (1%)	4.0 (42%)	5.4 (57%)	9.5 (99%)	9.6
SVN	0.12 (1%)	0.031 (<1%)	0.154 (2%)	2.2 (24%)	7.0 (74%)	9.2 (98%)	9.4
GRS	0.21 (6%)	0.050 (1%)	0.259 (7%)	1.0 (28%)	2.3 (65%)	3.2 (93%)	3.5
Total	1.61 (3%)	0.262 (<1%)	1.466 (2%)	30.3 (40%)	43.3 (58%)	73.5 (98%)	75.0

Values in parentheses represent the percent of total P demand (final column) met by each process (columns 2–7). DBF, deciduous broadleaf forest; DNF, deciduous needleleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRS, grassland; MIX, mixed forest; SHB, closed shrublands; SVN, savannas; and WSV, woody savannas.

Table 3. Total net primary production (MODIS NPP) and NPP from new nutrients by biome

Biome	Area, Mkm^2	Total NPP, Pg·C·y^{-1}	NPP from new N		NPP from new P	
			Pg·C·y^{-1}	% Total	Pg·C·y^{-1}	% Total
ENF	6.17	2.86	0.07 (0.07–0.09)	2.6 (2.3–3.1)	0.12 (0.07–0.13)	4.1 (2.5–4.5)
EBF	16.21	17.49	3.06 (2.01–4.15)	17.5 (11.5–23.7)	0.08 (0.07–0.16)	0.5 (0.4–0.9)
DNF	1.62	0.56	0.02 (0.02–0.02)	2.9 (2.9–2.9)	0.03 (0.03–0.03)	5.7 (5.2–5.7)
DBF	1.12	0.71	0.16 (0.05–0.31)	21.9 (6.4–43.4)	0.01 (0.01–0.02)	2.0 (1.0–2.2)
MIX	7.46	4.30	0.23 (0.08–0.42)	5.5 (1.9–9.7)	0.14 (0.07–0.14)	3.3 (1.7–3.3)
SHB	26.98	4.75	0.20 (0.11–0.38)	4.2 (2.4–8.0)	0.23 (0.21–1.05)	4.9 (4.4–22.1)
WSV	7.71	4.94	1.30 (0.12–2.14)	26.3 (2.5–43.2)	0.06 (0.04–0.09)	1.2 (0.7–1.7)
SVN	10.78	6.23	1.88 (0.18–3.36)	30.1 (2.9–53.9)	0.10 (0.04–0.14)	1.7 (0.7–2.3)
GRS	11.15	2.52	0.04 (0.01–0.13)	1.6 (0.5–5.1)	0.11 (0.09–0.24)	4.2 (3.6–9.5)
Total	88.20	44.35	6.87 (2.73–10.98)	15.7 (6.0–24.8)	0.89 (0.62–2.00)	2.0 (1.4–4.5)

The median values of within-biome spatial variability are reported for NPP from new nutrients. Values in parentheses represent the within-biome interquartile range in spatial variability. These estimates integrate the spatial variability observed in all internal and external nutrient inputs (Figs. S2 and S4). DBF, deciduous broadleaf forest; DNF, deciduous needleleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRS, grassland; MIX, mixed forest; SHB, closed shrublands; SVN, savannas; and WSV, woody savannas.

quantitative difference in values for new NPP from N versus P is also consistent with the idea that the P cycle is more closed than the N cycle, and suggests that, all else remaining equal, P acts as a more ultimate constraint on the mass-balance of nutrients that fuel global productivity on land (6). The distinction of P as an "ultimate constraint" on new plant productivity is consistent with the long-term view of nutrient limitation in the global ocean (32, 33).

Our estimates suggest that globally soil N and P mineralization rates of 696 Tg N·y^{-1} and 43 Tg P·y^{-1} (1 Pg = 10^{15} g) are both sufficient to meet 58% of annual plant N and P demands (Tables 1 and 2, Fig. S5). N:P mineralization ratios (Fig. 1*A*) decline from low to high latitudes, consistent with multiple studies suggesting relatively low foliar N:P ratios (34) and N limitation (4) in temperate and high-latitude ecosystems and relatively high foliar N:P ratios (35) and P limitation (4, 7) in many low-latitude, tropical ecosystems. The calculated average global N:P mineralization ratio (i.e., 16, generated from the data in Tables 1 and 2) is also strikingly similar to the Redfield ratio (106C:16N:1P) (32), matches well with previously published, independently derived, global empirical measurements of foliar N:P ratios (34–36), and is nearly identical to the hypothesized leaf N:P breakpoint between N limitation (N:P <14) and P limitation (>16) (37, 38). These similarities argue for the validity of our conceptual and analytical approaches, but we consider experiments focused on recycling ratios of N and P within and among terrestrial biomes, similar to those conducted for decades in different sectors of the global ocean (39), as a high research priority. Our analysis also provides an empirically based dataset for testing the skill of the current and future generations of global land surface models that aim to simulate total plant N and P uptake and the patterns and different sources of plant N and P across the terrestrial biosphere.

Our analysis also highlights important differences in the proportions of new versus recycled production from N and P. Globally, the amount of NPP attributed to new N inputs is equal to 6.87 Pg C·y^{-1} (2.72–10.98 Pg C·y^{-1}), meaning that ~16% of current global NPP is achieved via new N inputs (Table 3 and Fig. 1*B*), a proportion that is very similar to new N productivity in the global ocean (i.e., 18%) (14). By contrast, the fraction of terrestrial NPP that is met by new P inputs is much more modest (Table 3 and Fig. 1*C*), representing only ~2% of total global NPP (0.62–2.00 Pg C·y^{-1}). These differences make sense given the lack of both an N fixation analog and a common gaseous phase in the P cycle; small annual inputs of new P from weathering and P deposition are under less direct biological control, and thus inputs of new P are much more modest than inputs of new N. The implication of a relatively closed P cycle places added emphasis on the cycling and regulation of this element in constraining future NPP. For example, standard conceptual models suggest that much of the soil P in occluded forms is not available to terrestrial plants, yet plants have a number of mechanisms to liberate soil-bound P, including mycorrhizae, root exudation and chelation, and rhizosphere redox changes. These interactions (40), as well as those between N and P (41), have the potential to greatly enhance P availability. However, further research on P cycling and availability will be important to better understand and predict long-term patterns of terrestrial NPP.

The terrestrial C cycle strongly regulates the Earth's climate through the combined effects of both atmospheric C removal via photosynthesis and returns of CO_2 to the atmosphere via respiration. At present, the terrestrial biosphere is a strong sink for atmospheric CO_2, with estimates suggesting that from 1990–2000 annual C uptake via NPP on land exceeded respiratory losses by ~2.5 Pg C·y^{-1} (42–44). The location of this terrestrial C sink is poorly resolved (1, 45, 46), and the future trajectory of terrestrial C uptake rates is uncertain (46), but it is thought to be driven, at least in part, by enhanced plant productivity (47–49). The capacity for new plant production ultimately requires new nutrient inputs, and our results point to tropical biomes as having the greatest new N inputs via fixation, compensating for the large quantities of N lost via leaching and denitrification from this biome (50–52). N fixation is performed both symbiotically and asymbiotically in terrestrial ecosystems; conservation efforts that limit harvesting of N-fixing trees, or reducing soil erosion and associated losses of P minerals, will maximize new nutrient production on land. Finally, while Earth's biogeochemical cycles respond to multiple drivers (e.g., climate and atmospheric CO_2), areas with the highest new nutrient production are those where additional plant NPP is most likely to continue in the future. (Table 3 and Fig. 1 *B* and *C*).

Methods

We used a mass-balance framework to examine the proportions of new versus recycled terrestrial NPP:

$$NPP_{total}(N,P) = NPP_{new}(N,P) + NPP_{recycle}(N,P) \quad [1]$$

$$f_{new}(N,P) = \frac{NPP_{new}(N,P)}{NPP_{total}} \quad [2]$$

$$f_{recycle}(N,P) = \frac{NPP_{recycle}(N,P)}{NPP_{total}}, \quad [3]$$

where total NPP nutrient demand [$NPP_{total}(N,P)$] of a given nutrient (N or P) is assumed to equal the sum of NPP fueled by new nutrient inputs [$NPP_{new}(N,P)$] and recycled nutrients [$NPP_{recycle}(N,P)$]. We then calculated the fraction of

$NPP_{total}(N,P)$ met by new nutrient inputs [$f_{new}(N,P)$] and recycled nutrients [$f_{recycle}(N,P)$]. *SI Methods*, sections S1–S4 gives additional details.

We used 10-km^2 satellite-derived NPP data obtained from the Aeronautics and Space Administration's Moderate Resolution Imaging Spectroradiometer (MODIS NPP; Fig. S6), and to account for interannual variability, MODIS NPP was averaged over the 2000–2010 period. MODIS NPP data were strongly and significantly correlated ($r = 0.99$; $P < 0.0001$) with independent, empirically based estimates of NPP obtained from the Ecosystem Model–Data Intercomparison [EMDI NPP (53); Fig. S7]. We thus partitioned MODIS NPP into four distinct C pools (leaf C, shoot C, coarse-root C, and fine-root C) using published, biome-specific estimates of C allocation (Table S1), and calculated total terrestrial nutrient (N and P) demand by applying published biome-specific C:nutrient ratios (C:N and C:P) for each C pool (*SI Methods*, Fig. S8, and Table S1). Thus, the sum of leaf, shoot, coarse-root, and fine-root nutrient content represents current NPP nutrient demand (Fig. S9), and NPP nutrient demand represents the sum of new nutrient inputs and recycled nutrients (*SI Methods*, sections S1–S4). New N inputs were calculated using previously published estimates of N deposition (Fig. S1) as well as free-living and symbiotic N fixation (Fig. S1), and new P inputs as the sum of P deposition (Fig. S3) and soil mineral P weathering rates (Fig. S3). For both N and P, nutrient recycling was calculated as the sum of nutrient resorption (Table S1) and mineralization (Fig. S5). The proportion of NPP derived from new nutrient inputs (NPP_{new}) was computed at a 10-km^2 spatial resolution according to

$$NPP_{new}(N,P) = NPP_{total}(N,P) \times f_{new}(N,P). \qquad [4]$$

ACKNOWLEDGMENTS. We thank J. Dukes and the Steering Committee of the Integrated Network for Terrestrial Ecosystem Research on Feedbacks to the Atmosphere and Climate (INTERFACE) Research Coordination Network (Grant NSF-DEB-0955771) for funding the workshop that led to the development of these ideas and this manuscript. We thank E. Bai for providing data. We also thank D. Schimel for comments on the dataset and three anonymous reviewers for valuable input on early versions of the manuscript. C.C.C. and B.Z.H. acknowledge financial support from the A.W. Mellon Foundation.

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