

The Nitrogen Paradox in Tropical Forest Ecosystems

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Abstract

Observations of the tropical nitrogen (N) cycle over the past half century indicate that intact tropical forests tend to accumulate and recycle large quantities of N relative to temperate forests, as evidenced by plant and soil N to phosphorus (P) ratios, by P limitation of plant growth in some tropical forests, by an abundance of N-fixing plants, and by sustained export of bioavailable N at the ecosystem scale. However, this apparent up-regulation of the ecosystem N cycle introduces a biogeochemical paradox when considered from the perspective of physiology and evolution of individual plants: The putative source for tropical N richness—symbiotic N fixation—should, in theory, be physiologically down-regulated as internal pools of bioavailable N build. We review the evidence for tropical N richness and evaluate several hypotheses that may explain its emergence and maintenance. We propose a leaky nitrostat model that is capable of resolving the paradox at scales of both ecosystems and individual N-fixing organisms.

WHAT SUSTAINS NITROGEN RICHNESS IN TROPICAL FORESTS?

Tropical forests play a pivotal role in regulating Earth's climate and biogeochemical cycles through their vast exchanges of energy, water, carbon, and nutrients with the global atmosphere (Bonan 2008, Brown & Lugo 1982, Cleveland et al. 1999, Field et al. 1998, Melillo et al. 1993). Because of their high productivity, tropical forests account for a large proportion of global terrestrial carbon storage and cycling and are thought to play a critical role in buffering the atmosphere against rising CO₂ (Chave et al. 2008, Gerber et al. 2009, Lewis et al. 2009, Malhi & Phillips 2004, Phillips et al. 1998). Yet, despite the well-recognized importance of this biome to biogeochemistry as well as biological diversity, fundamental uncertainties remain in our understanding of the nutrient cycles that underlie the productivity and dynamics of these forests worldwide.

One of the most vexing problems lies in the resolution of the nitrogen (N) cycle across this vast biome. Although tropical forests are quite variable in biotic composition and functional properties, it is often assumed that humid lowland tropical forests generally are rich in N relative to other nutrients such as phosphorus (P) or calcium (Ca). This assumption is supported by evidence indicating that at least some tropical forests possess the capacity to build up, recycle, and export (via leaching and denitrification) very large quantities of N (e.g., Davidson et al. 2007, Hall & Matson 1999, Hedin et al. 2003, Houlton et al. 2006, Jenny 1950, Martinelli et al. 1999, Vitousek 1984, Vitousek & Sanford 1986). This capacity introduces a stark and fundamental contrast in our conception of forests as biogeochemical systems: Temperate forests are seen as subject to strong and persistent N limitation, whereas lowland tropical forests are viewed as possessing the exceptional capacity to develop abundant supplies of N. Is such a biome-scale dichotomy in N cycling real and, if so, what maintains it?

The view of lowland tropical forests as N rich is subject to two fundamental problems. First, the generalization is based on limited empirical information that often is indirect and nonexperimental. Second, and more fundamentally, it is theoretically difficult to resolve the emergence of N richness at the ecosystem level, based on mechanisms that operate at the level of physiology and ecology of individual N-fixing organisms. The most commonly offered explanation—that biological N fixation (BNF) brings in large amounts of new N from the atmosphere (e.g., Cleveland et al. 1999, Crews 1999, Galloway et al. 2004, Jenny 1950, Robertson & Rosswall 1986, Vitousek & Howarth 1991)—suffers from the problem that, at the organismal level, BNF ought to be down-regulated in N-rich environments (e.g., Barron 2007, Hartwig 1998, Menge et al. 2009a, Pearson & Vitousek 2001) and therefore cannot be invoked as a mechanism that can sustain richness in N over other resources (Hedin et al. 2003). Hedin et al. (2003) proposed that buildup of bioavailable N in humid tropical forests presents a major unresolved paradox in the terrestrial N cycle with implications for understanding how organisms function within ecosystems and how forests function within the global Earth system.

We here review the evidence for the idea that humid tropical forests can naturally develop high bioavailability of N relative to other resources. We also examine three competing mechanisms that individually, or in combination, can resolve this paradox of N richness in tropical forest ecosystems. Finally, we discuss some key challenges for the path toward better understanding of the N cycle in this important biome.

THE TROPICAL NITROGEN PARADOX

In 1950, Hans Jenny first raised the question of why some tropical forests appear to build up and recycle very large amounts of N (Jenny 1950). Based on the limited data available at the time, and using back-of-the-envelope calculations of soil nutrient turnover (Jenny et al. 1948, 1949),

Jenny inferred that humid tropical forests must depend on external N inputs that are substantially greater than those observed in temperate regions. What factor, asked Jenny, can sustain such large N inputs to tropical ecosystems, when conventional wisdom holds that N is an exceedingly rare resource that limits plant growth in many terrestrial ecosystems?

Jenny invoked a biological mechanism to explain this pattern: Symbiotic N-fixing plants—primarily in the family *Fabaceae* (*Leguminosae*)—act to bring in large amounts of new N from the atmosphere. Specifically, he argued that because symbiotic N fixers are both abundant and diverse in the tropics (but not in temperate regions), this unique plant group could supply the external N needed to sustain rich N availability at the ecosystem level.

We have learned a great deal about tropical nutrient cycles in the six decades following Jenny's seminal observations. We now know that the N content of soils varies greatly across terrestrial ecosystems worldwide, with relatively high stores occurring in moist and productive environments such as tropical and subtropical forests (Post & Pastor 1985). We also know that tropical forests can, over centuries to millennia of ecosystem development, become exceedingly rich in N relative to P and/or other plant resources (Harrington et al. 2001, Hedin et al. 2003, Herbert & Fownes 1995, Vitousek & Farrington 1997). Studies of tropical soils have similarly shown that N can build up to levels presumed to be in excess of other mineral resources, most notably P and base cations such as Ca (Cleveland et al. 2002, Crews et al. 1995, Fox et al. 1991, Hall & Matson 1999, Van Wambeke 1992, Wardle et al. 2004). In addition, recent observations show that some tropical forests appear to sustain substantial losses of bioavailable forms of N (Hedin et al. 2003, Houlton et al. 2006, Lewis et al. 1999) at rates that exceed those thought to be diagnostic only of highly polluted and N-saturated temperate forests. Finally, efforts to construct regional- or global-scale N budgets have generally accepted the presumption that BNF rates are high in tropical forests compared to their temperate, boreal, or arctic counterparts (Cleveland et al. 1999, Galloway et al. 2004, Robertson & Rosswall 1986). It should be noted, however, that these budget calculations derive from only a few field studies of BNF and other N fluxes, extrapolated to vast regions of the forested tropics.

Although these observations generally support the notion that N richness can develop in tropical forests, they raise two serious problems relative to Jenny's interpretation that this phenomenon is caused by high rates of symbiotic BNF. First, the field observations come from few studies in few locations, such that our knowledge of tropical nutrient cycles is geographically selective. This is particularly germane as tropical forests occupy an extraordinarily broad range of variation in biotic and abiotic factors including climate, biota, geological parent material, relief, soil conditions, and age and frequency of disturbances. Rather than being monolithic and static, these forests likely display considerable variation in plant-nutrient-soil dynamics, calling for careful use of abstraction and generalization (e.g., Grubb 1977; Herrera et al. 1978; LeBauer & Treseder 2008; Townsend et al. 2007, 2008; Vitousek 1984). We here review the strengths, limitations, and implications of the present evidence for N richness in tropical forests.

A second and conceptually deeper issue concerns the apparent paradox that is the central theme of this review: N fixation in the face of N richness (or, vice versa: N richness in the face of costly N fixation). While Jenny's idea of symbiotic BNF can help explain the emergence of N richness at the level of ecosystem dynamics, it fails to explain why fixation should be maintained physiologically, ecologically, and evolutionarily at the level of individual plants. Given the substantial energetic cost of BNF (Gutschick 1981), and given that N fixers must remain competitive against nonfixing plants, fixers ought to down-regulate fixation once N availability builds up in excess of demand in the local environment. Such facultative fixation is well recognized experimentally, in symbiotic fixers (Ingestad 1980, Olsen et al. 1975, Pate & Dart 1961) as well as in nonsymbiotic (heterotrophic) N-fixing bacteria in soils (Barron et al. 2009, Crews et al. 2000). The paradox of N richness therefore

identifies a fundamental contradiction across scales of biological organization: Though BNF can sufficiently resolve the emergence of N richness at the level of ecosystems, the explanation is inconsistent with theoretical expectations of how BNF should function as an adaptive strategy at the level of individual organisms.

McKey (1994) advocated a slightly different perspective by suggesting that the ecological benefits associated with the N-rich lifestyle of legumes (many of which are N fixers)—such as elevated photosynthetic capacity, N-rich seeds, or increased herbivore defense by N-rich compounds—may outweigh the costs of BNF even in habitats where soil N is sufficient for nonfixing plants. This perspective offers support for the idea that N fixers fix even when N availability is high and, as a result, fixation can be the major determinant of N-rich conditions in tropical lowland forests (Cleveland et al. 1999, Houlton et al. 2008, Jenny 1950). The perspective introduces the idea of overfixation, which we here define as fixation that is sustained even in the face of high N availability. Such overfixation can, in theory, maintain N inputs at the ecosystem scale, even beyond what is needed to alleviate N limitation.

Overfixation can result if fixers are physiologically unable to reduce BNF in environments with high bioavailable N. Obligate fixation is the, perhaps, most pure form of overfixation, in which fixers are incapable of adjusting BNF in response to any change in local levels of bioavailable N. Overfixation can also result from an imperfect feedback between BNF and N availability, such that down-regulation of BNF occurs only once N has accumulated well beyond N limitation. Although differing in magnitude, imperfect regulation and obligate fixation yield the same effect: maintenance of N fixation beyond what is needed to alleviate N limitation. In a competitive environment, such overfixation is likely energetically costly compared to the strategy of instantaneous, facultative down-regulation. It is therefore reasonable to expect strong selective pressure on the ability of individual fixers to fine-tune BNF to match local N availability, to the extent such fine-tuning is possible (Menge et al. 2008).

Using a simple ecosystem model, we next explore the influence of three alternative fixation strategies on the buildup and loss of bioavailable N at the ecosystem level: absence of N fixation, obligate overfixation (constant N fixation per unit plant biomass), or perfect facultative fixation (down-regulation of BNF once N limitation is alleviated). We then compare this analysis against empirically observed patterns of N cycling.

INFLUENCE OF FIXATION DYNAMICS ON ECOSYSTEM NITROGEN RICHNESS

Inputs of external N by fixation can have complex and even counterintuitive effects on the availability, cycling, and loss of N at the ecosystem level. Of particular concern is whether a dynamic feedback is established between fixation and local N availability. We here summarize the consequences of different fixation dynamics by showing simulation results from a plant-soil ecosystem model. Our analysis builds on earlier models (Menge et al. 2008, 2009a,b) by incorporating a second mineral nutrient resource in addition to N and allowing different dynamics of BNF. Although the second resource could be any growth-limiting nutrient, we here consider P because it is often assumed to limit plant growth in many tropical soils (Porder et al. 2007, Vitousek 1984).

As illustrated schematically in **Figure 1**, we let plant biomass growth (dB/dt) depend on uptake of bioavailable N (A_N) and P (A_P) from the soil and from N fixation (F), and we express the cost of N fixation as a reduction in net plant growth:

$$\frac{dB}{dt} = B(\text{MIN}\{\omega_N[v_N(A_N) + F], \omega_P v_P(A_P)\} - \mu - \theta F). \quad 1.$$

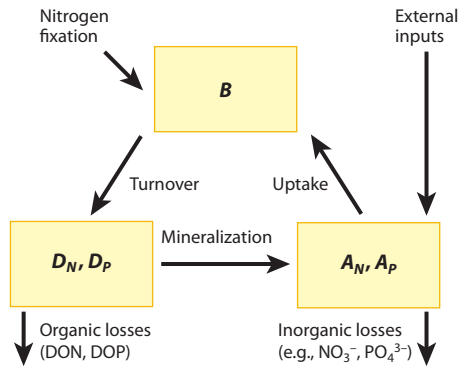


Figure 1

Model of ecosystem nutrient cycle of nitrogen (N) and a second mineral resource, in this case phosphorus (P). The model builds upon a family of models designed to evaluate ecosystem nutrient limitation (e.g., Daufresne & Hedin 2005; Menge et al. 2008, 2009a,b; Vitousek et al. 1998, Vitousek & Field 1999). Nutrients enter the ecosystem via atmospheric deposition (external inputs) and, in the case of N, via biological N fixation (nitrogen fixation). Nutrients exist in fixed quotas in plant biomass (*B*) and cycle within the ecosystem through a soil detritus (*D*) and a plant-available pool (*A*). Ecosystem losses occur either as bioavailable inorganic nutrients (e.g., nitrate and phosphate) from the plant-available pool or as unavailable dissolved organic nutrients (DON and DOP) that leach from the detrital pool (e.g., Hedin et al. 1995, 2003). Although our discussion considers mainly leaching losses of organic versus inorganic nutrients, other loss vectors can be added. For example, because denitrification depends on the bioavailable nitrate pool A_N , it can be treated similarly to hydrologic nitrate loss (Hedin et al. 2003). In contrast, volatile nitrogen losses from fire do not directly depend on A_N , but instead are equivalent to an increase in unavailable losses from the organic pool D_N .

The parameters ω_N and ω_P are plant-nutrient use efficiencies for N and P, $v_N(A_N)$ and $v_P(A_P)$ are saturating uptake functions of bioavailable N and bioavailable P, μ is the plant biomass turnover rate, and θ is the carbon cost of N fixation.

At the ecosystem level (**Figure 1**), we distinguish two paths of N loss that are key for understanding nutrient availability and the emergence of nutrient limitation on plant growth (Gerber et al. 2009; Hedin et al. 1995, 2003; Menge et al. 2009b; Neff et al. 2004; Perakis & Hedin 2002; Vitousek et al. 1998): losses that originate from the plant-available pool of inorganic nutrients (A_N in **Figure 1**) versus those that originate from the plant-unavailable pool of organically bound soil nutrients (D_N). Although we focus on hydrological losses—that is, of dissolved nitrate from the bioavailable pool, and of dissolved organic N (DON) from the soil organic pool—losses from the plant-available pool can also occur as gaseous N emitted by soil transformations such as denitrification (e.g., Hedin et al. 2003, Houlton et al. 2006). In addition, fire can promote volatile losses of unavailable N from organic pools. The dynamics of total N (T_N) within the ecosystem are given by the balance of inputs and these two losses:

$$dT_N/dt = I_N + BF - k_N A_N - \varphi_N D_N. \quad 2.$$

Here, I_N is the non-BNF input flux (that is, atmospheric deposition), k_N is the loss rate of bioavailable N, and φ_N is the loss rate of unavailable N. Equation 2 can be derived from equations 1, 2, and 4 in Menge et al. (2009a); consult this reference for a full description and analytical treatment of the model.

We show in **Figure 2** that N availability, nutrient limitation, and patterns of N loss depend dramatically upon the dynamics by which external N enters the ecosystem. If BNF is absent (that is, $F = 0$) in an unpolluted environment (that is, subject to low N deposition), plant biomass tends

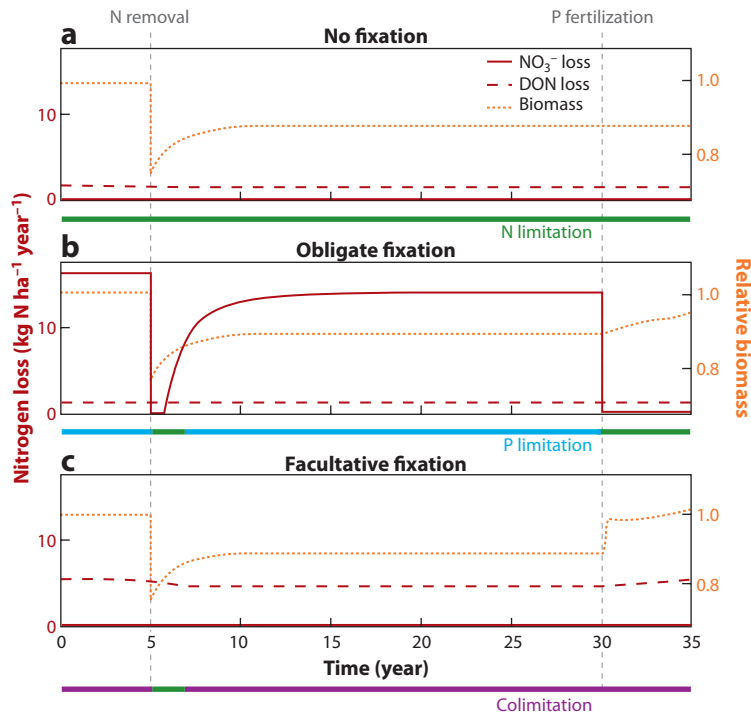


Figure 2

Simulations showing responses of nitrogen (N) losses, plant biomass, and nutrient-limitation status to a disturbance that causes N removal and to phosphorus (P) fertilization. Each panel assumes different dynamics of N inputs through symbiotic fixation: (a) no fixation, (b) obligate N fixation, and (c) perfect facultative N fixation. Hydrological losses of bioavailable (nitrate; red solid line) and unavailable (DON; red dashed line) forms of N are shown on the left axis, whereas biomass is displayed on the right axis (orange hatched line). The line below each panel displays the limitation status of plant growth: N-limited (green), P-limited (light blue), or colimited by both N and P (purple). The model starts at equilibrium, then at 5 years, we remove 25% of plant N and 5% of soil N. After quasi-equilibrium is established, we fertilize with 100 kg ha⁻¹ of P at 30 years.

to be limited by N and remains N-limited when subjected to either N removal from the internal cycle or increased P input (**Figure 2a**). In addition, plant-available N (A_N) remains scarce, and hydrological losses are low and dominated by dissolved organic forms of unavailable N over bioavailable N. This condition is characteristic of unpolluted temperate forests that are subject to strong N limitation (e.g., Hedin et al. 1995, 2003; Perakis & Hedin 2002; McGroddy et al. 2008).

If BNF is obligate (that is, $F > 0$ and F is constant in Equations 1 and 2), however, then overfixation is common and significant amounts of N build up in the plant-available pool (A_N), causing high and sustained ecosystem losses of nitrate over dissolved organic N (**Figure 2b**). In this case, plant biomass responds positively to increased P input, and remains limited by P with the exception of a short period following internal N removal.

If BNF instead is perfectly facultative, such that it occurs only in N-poor conditions (that is, F depends inversely on A_N in Equation 1), then plants never overfix and fixation acts to equilibrate plant N and P acquisition relative to demand over a wide range of N and P availabilities (**Figure 2c**). Plant growth thus remains colimited by both nutrients, and biomass is responsive to both N removal and increased P input. As a result, ecosystem N losses are greater than in the no-fixation

scenario, but differ from the obligate scenario in that these losses are composed entirely of dissolved organic N rather than bioavailable nitrate.

This comparative analysis illustrates that up-regulation of N availability above the availability of a second resource such as P, and beyond colimitation, depends on overfixation (**Figure 2b**) and cannot be sustained by a facultative mechanism that equilibrates N demand relative to P. The analysis formally shows the difficulty of reconciling the idea of Jenny and others after him—that N fixation can sustain N richness and P limitation via overfixation—with the competing idea that N fixation is a costly, facultative plant strategy. Of note is the emergent prediction that perfectly facultative fixation should, over time, act to equilibrate N to P and/or other resources in limited supply (**Figure 2c**). This prediction of colimitation is conceptually analogous to Alfred Redfield's influential idea that fixation acts to equilibrate N and P levels in the global ocean, at or near the ratio required by algal growth (Redfield 1958). However, because Redfield's mechanism operates at the level of entire algal communities that turn over rapidly, equilibration between N and other resources may occur by community-level changes in relative abundances of fixers versus nonfixers. In contrast, the BNF-soil feedback occurs at timescales shorter than the life span of trees in forested communities, such that facultative down-regulation at the level of individual plants is the most likely mechanism that adjusts N relative to other resources.

Although empirical measures are limited, tropical forests are generally not thought to be colimited by N and P or any other mineral resource. We next examine the empirical evidence for N richness relative to other resources in tropical forests.

ECOSYSTEM-LEVEL EVIDENCE OF NITROGEN RICHNESS

Information about the bioavailability of nutrients in tropical forests comes from indirect observations of nutrient levels in soils, foliage, and litter; from direct nutrient manipulation experiments; and from ecosystem-scale measures of nutrient losses. Early studies considered total contents of nutrients in soils and plant tissues as an indication of availability to plants (e.g., Ewel 1976, Greenland & Kowal 1960, Grubb 1977, Herrera et al. 1978, Jenny 1950, Jenny et al. 1948, Nye 1961). These studies noted high levels of N relative to other resources in both soils and plants. For example, Nye (1961) reported high concentrations of N in tropical litter compared to temperate biomes. In their comparison of major nutrients (N, P, Ca, etc.) in soils and vegetation across Fittkau's (1971) "ecological subregions" of the Amazon Basin (**Figure 3a**), Herrera et al. (1978) reported especially low contents of P and Ca relative to N and other nutrients. More recent analyses have questioned whether nutrient ratios from individual species—which can vary substantially across taxonomic affiliation—can be used to indicate variations in soil nutrient availability (Townsend et al. 2007). At the ecosystem level, however, plant P content appears to be responsive to local differences in soil P (Kitayama & Aiba 2002, Nardoto et al. 2008, Richardson et al. 2008, Santiago et al. 2005, Silver 1994). By analyzing more than 1000 trees in 63 plots across the Amazon Basin, Fyllas et al. (2009) showed that foliar P, Ca, and K were strongly influenced by local growing conditions, whereas N largely varied with taxonomic affiliation. This apparent lack of variation in N (also shown in Nardoto et al. 2008, Richardson et al. 2008, Santiago et al. 2005) may indicate that N often is available in excess relative to P.

There were considerable efforts in the 1970s and 1980s to characterize plant-soil nutrient relations across tropical forests; this information is summarized in several critical reviews (Grubb 1989, Högberg 1986, Richter & Babbar 1991, Sanchez 1976, Vitousek & Sanford 1986). The emerging early view was that forests on highly weathered soils (oxisols/ultisols or ferrasols/alisols) often display high N but low P and Ca contents, whereas montane (and perhaps riverine) forests are comparably less rich in N.

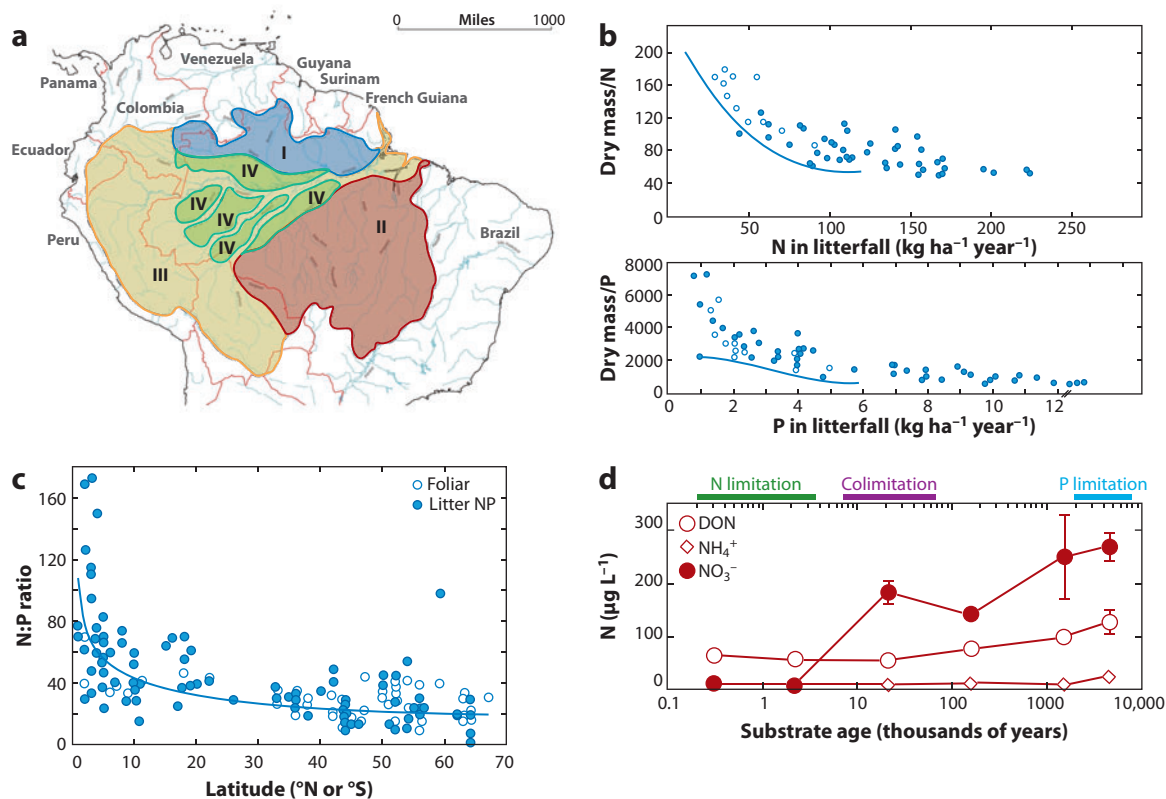


Figure 3

Different indications of N richness across tropical forests. (a) Early studies focused on variations in nutrient contents of soils and plants across tropical forests. For example, Herrera et al. (1978) compared concentrations of macronutrients in soils and plants across four broad ecological subregions within the Amazon Basin (Fittkau 1971): I, Guyana Shield (infertile and highly weathered soils); II, Brazilian Shield (infertile and highly weathered soils); III, Western Periferal Amazonia (heterogeneous collection of more fertile and less weathered soils); IV, Central Amazonia (infertile areas of sediments deposited from the Guyana and Brazilian Shields). The map is from Quesada et al. (2009). (b) Vitousek analyzed the efficiency of litterfall nutrient use (expressed as dry mass/nutrient weight ratio) as a function of the annual rate of above-ground circulation (in kilograms per hectare per year) of a given nutrient across 62 native and planted tropical forest stands. The top panel displays how N-use efficiency declines as internal N circulation increases, following a pattern similar to the trend observed across temperate and boreal forests (*solid regression line*). The bottom panel shows how P-use efficiency declines with increasing P circulation. Values are higher in tropical forests with low rates of P circulation compared to their temperate counterparts (indicated by the *solid line*). Individual points signify montane (*open circles*) and lowland (*closed circles*) forests. Adapted from Vitousek (1984). (c) McGroddy and colleagues analyzed molar N:P ratios in foliage (*open circles*) and in litterfall (*solid circles*) in forest ecosystems across a latitudinal gradient. Both foliage and litterfall N:P ratios increased significantly ($p < 0.001$) with decreasing latitude. The trend was most strongly expressed in litterfall, with a highly nonlinear increase in N:P ratios with decreasing latitude (indicated by *solid regression line*; $p < 0.001$, $r = 0.43$). Adapted from McGroddy et al. (2004). (d) Patterns of hydrological N loss closely follow the nutrient limitation status of Hawaiian tropical forests over a four-million-year gradient in substrate development. Forests in which plant growth was demonstrably N-limited (indicated by *thick green line*) (Vitousek & Farrington 1997) displayed low to negligible losses of bioavailable nitrate (*closed circles*) and ammonium (*open diamonds*) combined with significant levels of unavailable dissolved organic N (*open circles*). In contrast, forests in which plant growth was demonstrably colimited by N and P or solely limited by P (*purple and blue thick lines*, respectively) displayed high losses of nitrate relative to dissolved organic nitrogen. Ammonium is not a common dissolved N form and remained low across all sites. Error bars signify 1 SE of the mean. From Hedin et al. (2003).

Despite this rather large body of information, it is problematic to generalize about biological availability based solely on nutrient contents of soils and/or plants. In their excellent early review, Vitousek & Sanford (1986) argued that static pools of soil N (or P) cannot be taken as adequate measures of bioavailability. More direct measures, such as rates of soil N (or P) mineralization, are still problematic as they fail to account for the nutrient demand imposed by plant growth—a term that can vary considerably with stand development, below-ground microbial processes, and species composition. In addition, measuring in situ mineralization of P, Ca, and other nutrients is methodologically difficult and, thus, rarely reported. As a result, measures of soil nutrients most often are too indirect and too incomplete to resolve their bioavailability to plants.

Vitousek (1984) offered a more sophisticated analysis by considering the total magnitude of nutrients that circulate in litterfall at the level of entire forest stands. He reasoned that if a nutrient is limiting to plant growth at the stand level, the nutrient use efficiency (NUE, ratio of dry mass to nutrient) in litterfall should be high in forests that experience low rates of circulation of that nutrient from plants to soils and back. As the availability of the nutrient increases (signified by increased internal circulation), nutrient limitation should disappear at the stand level, and the efficiency of nutrient use should decrease.

Vitousek's analysis suggested that efficiencies of N use are roughly similar in tropical versus temperate forests and that values seem to decrease in a similar pattern with increasing N circulation across both forest types (**Figure 3b**). In the case of tropical forests, high N-use efficiency values were largely associated with montane or white-sand forests that experienced low rates of N circulation. Most lowland tropical forests displayed consistently low N-use efficiency. In the case of P, however, high nutrient use efficiency occurred in both montane and lowland tropical forests subject to low rates of P circulation. This subset of forests displayed dry mass to P ratios that exceeded values from temperate and boreal forests (*solid line* in **Figure 3b**). However, most other forests displayed consistently low values of P efficiency, similar to temperate forests, and experienced higher rates of P circulation. From these patterns, Vitousek inferred that P rather than N most likely limits plant growth in a subset of tropical forests. Tanner et al. (1998) have extended this argument by suggesting that P limitation ought to dominate in lowland forests and N limitation in montane forests across the tropics.

McGroddy et al. (2004) offered an analogous but more direct analysis of forest stand-level N and P contents across latitudes worldwide. They reported a significant increase in canopy N:P ratios with decreasing latitude (a pattern also found across individual tree species; Hedin 2004, Reich & Oleksyn 2004), and an even more dramatic increase in litterfall N:P in many low-latitude tropical forests (**Figure 3c**). This analysis also suggests that N tends to be abundant relative to P across many tropical forests.

A limitation of both these analyses is that they seek to generalize across forests that are demonstrably variable. For example, while it is true that the ratio of dry mass to P is greatly elevated in tropical forests subject to low rates of internal P circulation, it is also true that this high ratio applies only to a limited subset of forests in the total dataset and that the remaining forests (especially those with higher P circulation) surprisingly do not differ much from their N-limited temperate counterparts (**Figure 3b**). Similarly, it is clear that while some forests at low latitudes display very high litterfall N:P ratios, several other forests do not (**Figure 3c**). From the perspective of this review, it is therefore difficult to judge the degree to which different tropical forests are constrained by P but rich in N (consistent with obligate fixation in **Figure 2b**), poor in N (consistent with lack of fixation in **Figure 2a**), or perhaps colimited by both N and P (consistent with facultative fixation in **Figure 2c**).

Nutrient manipulations offer a uniquely direct way to examine plant nutrient limitation, yet such experiments have been limited to only a handful of locations worldwide and have offered a

complex picture of the tropical N cycle. Experiments have shown P limitation and abundance of N in geologically old and P-poor Hawaiian soils (Vitousek & Farrington 1997), N limitation in geologically young Hawaiian soils (Vitousek & Farrington 1997), combined N and P limitation in Jamaican and Venezuelan montane forests (Tanner et al. 1990, 1992), combined N and P limitation in Amazonian secondary forests on P-poor oxisols (Davidson et al. 2004), and N limitation on seed and fruit production without any clear nutrient effect on plant biomass growth in Panamanian forests (Kaspari et al. 2008). In central African lowland rainforests, additions of P failed to stimulate both tree growth and seedling establishment (Newbery et al. 2002). Similarly, both N and P failed to stimulate growth in primary lowland forests of Borneo, although litterfall increased in response to both nutrients (Mirmanto et al. 1999). It is difficult to interpret these diverse results, in part because they derive from few locations, but also because, with the exception of Newbery's and Mirmanto's work, experiments are critically lacking from P-poor soils that are commonly found in lowland tropical regions.

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A direct signal of forest N status comes from the patterns of ecosystem N loss, based on the model predictions in **Figure 2**. Such analysis benefits from a much larger and more nuanced dataset than that of fertilization experiments. We here focus on patterns of dissolved losses of bioavailable nitrate or gaseous N losses from the denitrification of nitrate following the approach of Hedin et al. (2003). The idea is that in N-limited conditions, forests should export primarily unavailable forms of N such as DON and little nitrate or gaseous N, as illustrated in **Figure 2a**. In N-replete conditions, however, forests should export noticeable amounts of nitrate or gaseous N in addition to DON, as indicated in **Figure 2b** (Hedin et al. 1995, Menge et al. 2009b, Perakis & Hedin 2002, Vitousek et al. 1998).

Hedin et al. (2003) confirmed this expected pattern of N loss across a four-million-year-substrate age gradient in the Hawaiian islands (**Figure 3d**): Demonstrably N-limited forests on geologically young (<20,000 years) substrates did not export significant nitrate or gaseous N, whereas demonstrably P-limited forests on older substrates exported substantial amounts of N as nitrate and gaseous N relative to DON. These findings illustrate not only that ecosystem N losses reflect nutrient limitation status, but also that tropical forests can become very rich in N over developmental time (millennia or longer) and can sustain significant rates of N export (likely up to 10–15 kg N ha⁻¹ year⁻¹; Hedin et al. 2003, Houlton et al. 2006). We conclude that patterns of N loss appear to constitute a straightforward and direct way to evaluate N richness relative to other resources within and across forested ecosystems.

Additional observations of nutrient fluxes in tropical forests offer support for the idea that losses of dissolved nitrate are high in many tropical forests (Biggs et al. 2004, Forti et al. 2000, Lesack 1993, McDowell & Asbury 1994, Neill et al. 2001, Pringle et al. 1990, Ramos-Escobedo & Vazquez 2001, Schrumph et al. 2006, Wilcke et al. 2001, Williams et al. 1997). Newbold et al. (1995) documented large sustained losses of nitrate (4–6 kg N ha⁻¹ year⁻¹) and of total dissolved N (6–10 kg N ha⁻¹ year⁻¹) across six undisturbed Costa Rican watersheds, over a period of three years. Lewis et al. (1999) showed that undisturbed tropical forested watersheds often display significant nitrate losses, with total dissolved N export ranging up to 5–10 kg N ha⁻¹ year⁻¹.

In addition, direct field measures suggest that rates of gaseous N loss can be exceedingly high in tropical forests compared to their temperate and boreal counterparts (Hall & Matson 1999, Hedin et al. 2003, Matson & Vitousek 1987, Robertson & Tiedje 1988, Vitousek & Matson 1988). Finally, a complete isotopic input-output budget across several Hawaiian rainforests revealed the existence of sustained gaseous N losses on the order of 2–9 kg N ha⁻¹ year⁻¹, which, in combination with

dissolved N losses, caused total N export up to about 15–18 kg N ha⁻¹ year⁻¹ (Houlton et al. 2006).

To summarize, these observations suggest that export of bioavailable N (e.g., dissolved nitrate), and/or export via pathways that depend on bioavailable N (e.g., gaseous N), is relatively common in tropical forests and that it can occur in substantial quantities in some forests. Although our analysis indicates a propensity for tropical forests to develop N-rich conditions, it does not offer an explanation of how these losses are maintained nor does it resolve the paradox of whether BNF is the responsible factor.

PARADOX RESOLUTION

At heart, the paradox of tropical N richness considered in this review is caused by the lack of mechanistic resolution between perspectives on plant–nutrient interaction at the level of ecosystems versus the level of physiology and ecology of individual N-fixing plants. We observe high rates of N loss at the ecosystem scale, which, in turn, implies the existence of large N inputs from a source external to the ecosystem. BNF has been proposed as a likely candidate (Cleveland et al. 1999; Galloway et al. 1995, 2004; Houlton et al. 2008; Jenny 1950), but such sustained inputs are inconsistent with theories suggesting that individual N-fixing plants ought to down-regulate fixation in N-rich soil environments.

What is needed is an explanation capable of resolving the underlying mechanisms at both the ecosystem and individual levels. Such an explanation may or may not invoke BNF as the primary mechanism. One alternative explanation is that atmospheric N deposition may deliver sufficient external N to tropical biomes. High levels of N deposition could act to maintain N availability above other resources and, thus, bring about sustained export of dissolved nitrate. A second alternative is that our conception of the present-day dynamical state of the tropical N cycle might be in error. Specifically, bioavailable N losses could be sustained by the existence of a significant net imbalance in the large internal N stores of tropical forests, without the need to invoke any input of corresponding magnitude.

A different point of view is offered by the proposition that high rates of N fixation are sustained in P-poor and N-rich tropical forests because N fixation may enhance a plant's competitive ability for P (Houlton et al. 2008). However, though P-poor conditions can easily explain P limitation, they cannot easily explain the overabundance of bioavailable N in tropical forests. Maintenance of N richness over P or any other resource demands significant inputs of external N by a process that does not down-regulate at high N availability, such as obligate or overfixation (**Figure 2b**) or large atmospheric deposition fluxes.

We next evaluate three specific mechanisms that individually or in combination can resolve the apparent paradox of N richness: (a) biological N fixation, (b) atmospheric N deposition, and (c) ¹⁵N cycle disequilibrium.

HYPOTHESIS 1: BIOLOGICAL NITROGEN FIXATION

A necessary condition for BNF to serve as the key driver of N richness is the presence of putative N fixers. In an early review of African forests, Höglberg (1986) pointed out that taxa of N-fixing trees range from common to rare in humid forests of west and central Africa. In **Table 1**, we show the distribution and abundance of legumes across different tropical forests worldwide using an established network of 50-ha tree diversity plots (Losos & Leigh 2004). This analysis shows that while legumes are present in many forests at greater than 2% of total basal area, they are abundant in some forests but virtually absent in others.

Table 1 Legume abundance in 50-ha plots of various tropical forests worldwide. From Losos & Leigh (2004).

Site	% Basal area	% Trees
Barro Colorado Island, Panama	9.9	7.5
La Planada, Columbia	6.3	5.8
Luquillo, Puerto Rico	6.5	2.7
Yasuni, Ecuador	14.9	13.0
Ituri-Lendo, Democratic Republic of Congo	74.4	11.3
Ituri-Edoro, Democratic Republic of Congo	42.4	15.6
Korup, Cameroon	9.0	5.9
Mudumalai, India	2.4	19.3
Bikut Timah, Singapore	3.5	0.9
Doi Inthanon, Thailand	*	*
Huai Kha Khaeng, Thailand	*	3.1
Palanan, Phillipines	2.3	1.7
Nanjenshan, Taiwan	*	*
Lambir, Malaysia	2.1	2.1
Pasoh, Malaysia	8.5	3.3
Sinharaja, Sri Lanka	*	11.0

*Legumes not present in top 10 families.

This heterogeneity in legume abundance undermines leguminous BNF as a unifying mechanism to explain N-rich tropical systems. We note, however, that relatively little is known about the N cycle and nutrient limitation in the 50-ha plots in southeast Asia, the sites in **Table 1** where legumes are virtually absent. Moreover, measures of legume abundance may overestimate the potential for N fixation because many legumes cannot fix N. Nodulation is generally thought to be a generic trait (Sprent 2009). Within subfamilies roughly 54% of genera in *Mimosoideae* and 62% in *Papilionoideae* can fix N, whereas only 5% of genera in *Caesalpinioideae* are capable of doing so (de Faria & de Lima 1998, de Faria et al. 1989, Moreira & Franco 1994, Sprent 2005). Sprent (2009) described major differences in distribution of legume genera across equatorial rainforests in South America, Africa, and Asia, combined with differences in ability to fix N across different legume genera. Sprent notes that, though less studied, many African legumes are from taxa that are not likely able to fix N. For example, the Congo River basin contains forests that are dominated by legumes, but the most common species is a nonfixing *Caesalpinoid* (Högberg 1986).

We also examined McKey's idea that symbiotic N fixers should have higher foliar N contents than nonfixing plants. By comparing nine common tropical families, Townsend et al. (2007) documented elevated foliar N in legumes (*Fabaceae*) versus nonlegumes, but no clear taxonomic differences in P. Studies from native tropical forests have similarly shown that foliage N tends to be higher in legumes versus nonlegumes (Martinelli et al. 1999, Nardoto et al. 2008, Thompson et al. 1992). In their analysis of foliar properties across the Amazon Basin, Fyllas et al. (2009) reported higher N and P in foliage from N fixers than nonfixing taxa, but small to nonexistent differences between N-fixing versus nonfixing legumes. Both Townsend et al. and Fyllas et al. point out that there exist large differences in foliar N and P across tropical plant taxa, such that comparisons between fixing versus nonfixing plants must be placed in the context of broader taxonomic variation before inferring ecological and evolutionary implications.

For forests where putative N-fixing trees are abundant, we sought to evaluate field evidence for whether BNF is obligate or facultative with respect to N availability. Direct observations show that nodules can range from abundant to rare across forests, but we have little to no understanding of factors that govern this variation (de Faria & de Lima 1998, de Faria et al. 1989, Moreira & Franco 1994, Moreira et al. 1992, Norris 1969). From his observations in Congo, Bonnier (1958) noted that trees in intact forests rarely were nodulated, but that nodulation was common in recently disturbed habitats—as expected for facultative fixation. Similar reports of limited nodulation in intact forests come from Amazonia (Norris 1969, Sylvester-Bradley et al. 1980) and elsewhere (Beirnaert 1941, Keay 1953; both cited in Robertson & Rosswall 1986). Studies of *Acacia koa* in Hawaii show that BNF can drop rapidly after stand-level disturbance and is coincident with increasing soil-bioavailable N (Pearson & Vitousek 2001)—which is, again, consistent with facultative fixation.

Field measures across a natural gradient of N availability in native Panamanian rainforests revealed high rates of nodulation and fixation in recently disturbed (either direct physical disturbance or flooding) and N-poor forests, as well as in areas of disturbed forest gaps (Barron 2007). In contrast, Barron found nodulation and fixation to be virtually absent from undisturbed old-growth forests, despite an abundance of N-fixing legume species. This landscape-level pattern is consistent with facultative fixation in response to local variations in N availability.

Nevertheless, legume nodulation can be significant in forests subject to seasonal flooding (Bordeleau & Prevost 1994, Moreira et al. 1992, Saur et al. 2000) and in physically disturbed *terra firme* forests (Barron 2007, Moreira et al. 1992). Sprent (2001) reported a rare example of several genera of nodulating legume trees and lianas in a Cameroon forest, with nodules occurring in the uppermost and thin soil layer of organic plant litter (J.I. Sprent, personal communication). As a whole, these field observations suggest that nodulation is rare unless soils are low in N due to denitrification and leaching associated with flooding or physical disturbance. In addition, depletion of N relative to P in the organic-rich litter layer of soils may promote a local biogeochemical niche that induces N fixation (Barron et al. 2009, Menge & Hedin 2009).

Small-scale potted-plant experiments with tropical legume seedlings have nearly exclusively shown facultative down-regulation of nodulation and fixation at high soil N, often to the point of complete inhibition (e.g., McHargue 1999, Pons et al. 2006, van Kessel & Roskoski 1983). Pons et al. (2006) reported substantial but imperfect (that is, some fixation persisted in high N conditions) down-regulation in the case of one species grown in conditions of combined high levels of N and P. In contrast, field studies from temperate forests suggest that N-fixing trees such as *Alnus* and *Coriaria* may not appreciably down-regulate fixation in conditions of high soil N availability (Binkley et al. 1992, Menge & Hedin 2009), which is a pattern consistent with obligate or over fixation (**Figure 2c**). It may be relevant to note that these fixers depend on symbioses with bacteria of a different taxonomic identity than that of legumes.

It is more difficult to interpret evidence of N fixation from analyses of natural abundances of ^{15}N stable isotopes across individual trees. Such analyses have led to various conclusions, from reports of substantial fixation in tropical forests of French Guyana and Guyana (Pons et al. 2006, Roggy et al. 1999) to suggestions of little or no fixation in lowland rain forests of Cameroon (Högberg 1997). The approach assumes that N fixation can be calculated from a simplified isotope mixing equation between two distinct end members: atmospheric N_2 and soil N. However, this assumption likely oversimplifies the considerable complexity observed in ^{15}N across different soil N pools and fractionating paths of the plant-soil N cycle (Boddey et al. 2000, Evans 2001; Högberg 1997; Houlton et al. 2006, 2007). That ^{15}N signatures of nonfixing plant species often differ by 4–6 per mil in a single location indicates the lack of a distinct soil end member. From the perspective of this review, we therefore consider the ^{15}N approach promising but, at present, insufficient for clearly resolving N fixation at the individual plant level.

Although limited in scope, the available evidence from tropical trees suggests that facultative N fixation may be a fairly widespread strategy among leguminous fixers. The virtual absence of fixation in N-rich old-growth forests, combined with strong down-regulation in potted plant experiments, suggests that many plants follow a finely tuned strategy of perfect facultative fixation (**Figure 2c**). Because evidence from field studies is so limited, however, we cannot rule out overfixation as a common strategy. Symbiotic fixation by trees could still help resolve the N paradox if the facultative response is imperfect, such that overfixation takes place in N-rich conditions. For instance, time lags inherent in the physiological regulation of BNF might in a variable environment yield periods of overfixation (Menge et al. 2009a), even when individual plants seek to minimize the energetic costs of N fixation.

Information from nontree N fixers is even sparser. Little is known about lianas (Sprent 2001). Nonsymbiotic fixation by free-living heterotrophic bacteria is primarily restricted to shallow soils and the organic litter layers that covers these soils (Barron et al. 2009, Reed et al. 2008, Sprent & Sprent 1990, Vitousek et al. 2002). While rates of heterotrophic fixation typically are low compared to actively fixing legumes, such fixation can nevertheless bring in significant quantities of external N to ecosystems: up to $\sim 12 \text{ kg N ha}^{-1} \text{ year}^{-1}$ in some locations of wet Costa Rican lowland forests (Reed et al. 2008). Field studies have shown that heterotrophic fixation can be down-regulated by additions of N fertilizer (Barron et al. 2009, Crews et al. 2000; but see Reed et al. 2007) and that rates may also be controlled by molybdenum in some tropical soils (Barron et al. 2009) and P in others (Reed et al. 2007).

Fixation by canopy N fixers—epiphytic cyanolichens, cyanobacteria in bryophytes, and free-living bacteria on epiphylls—can also contribute significant external N inputs to tropical forests (up to $\sim 5 \text{ kg ha}^{-1} \text{ year}^{-1}$; Benner et al. 2007, Freiberg 1998, Matzek & Vitousek 2003, Reed et al. 2008). Benner & Vitousek (2007) demonstrated that abundances of N-fixing cyanolichens were influenced by long-term fertilization of montane Hawaiian soils. Although epiphytes appeared to respond to increased P availability on canopy surfaces (mediated by plant uptake and foliar leaching), there was no clear overall response to N addition. Matzek & Vitousek (2003) noted a similar lack of response of epiphytic fixers to changing soil N along a Hawaiian substrate age gradient, as did Menge & Hedin (2009) along a New Zealand substrate age gradient of temperate forests.

HYPOTHESIS 2: ATMOSPHERIC NITROGEN DEPOSITION

Studies of polluted temperate forests have shown that chronic N deposition can trigger export of substantial amounts of nitrate from watersheds that otherwise would not naturally leak nitrate (Aber et al. 1998, Perakis & Hedin 2002). It is difficult to extend these findings to tropical forests because—with the exception of local pollution hot-spots—rates of N deposition are thought to be low. A recent atmospheric model suggests that preindustrial N deposition was only slightly higher in tropical forests than that of temperate forests ($< 2.5 \text{ kg N ha}^{-1} \text{ year}^{-1}$; Galloway et al. 2004, Dentener et al. 2006), and that present-day values have increased further (up to $5 \text{ kg N ha}^{-1} \text{ year}^{-1}$). Values can be substantially higher downwind of dryland regions of Africa and South America, which burn frequently.

Direct measures of deposition are few and subject to variations in quality, preservation, and/or local emissions such as biomass burning, cattle farming, and agricultural fertilizer. Boy et al. (2008) reported a strong correlation between N deposition and biomass burning in an Ecuadorean montane forest, with more than half of total deposition ($\sim 10 \text{ kg N ha}^{-1} \text{ year}^{-1}$) caused by burn events. Markewitz et al. (2006) reported nitrate deposition at $0.1\text{--}2.5 \text{ kg N ha}^{-1} \text{ year}^{-1}$ across 17 individual studies throughout the Amazon Basin. Ammonium deposition was reported in the range of $0.6\text{--}4.7 \text{ kg N ha}^{-1} \text{ year}^{-1}$, and total inorganic deposition was in the range of

1.5–5.5 kg N ha⁻¹ year⁻¹. Ammonia generally does not travel far from the emission source before it is returned by wet or dry deposition. The ammonium component of deposition might therefore not represent new N from a source external to large forested regions, but rather recycled N similar to the distinction that marine biogeochemists make between new N delivered by external upwelling versus recycled N delivered by internal N mineralization.

The emergence of N pollution in some tropical areas may offer additional N inputs, but it appears unlikely that such local and recent effects are sufficient on their own to explain the existence of geographically broad trends in the tropical N cycle. Although atmospheric inputs of <5 kg N ha⁻¹ year⁻¹ may be enough to sustain nitrate losses from some tropical forests, the fluxes do not appear large enough for other forests. Deposition may therefore serve as an important background N source, but a significant additional source is needed to generate richness and loss of N from many tropical forests.

HYPOTHESIS 3: ECOSYSTEM DISEQUILIBRIUM

It is possible that the tropical forest N cycle simply does not follow the traditional assumption of quasi-balance between losses and inputs over longer time periods. We can envision scenarios in which ecosystem N losses exceed inputs, and which could generate losses of bioavailable N, albeit over a transient period. Such nonequilibrium effects may be caused by changes in factors such as atmospheric CO₂, climatic conditions, or rates and nature of disturbances. Increasing CO₂ does not favor ecosystem N losses, however, as accelerated forest growth in response to CO₂ fertilization only serves to increase demands and retention of N in ecosystems. Such accelerated forest growth has been documented across broad regions of Amazonia and Africa (Lewis et al. 2009, Phillips et al. 1998).

Very little is known about the sensitivity of tropical N cycles to variations in climate associated with El Niño/Southern Oscillation, migration of the intertropical convergence zone, or similar dynamics (Haug et al. 2001). It is clear, however, that tropical forests are affected by broad climatic trends such as increased temperatures and decreased moisture in African montane forests (Hemp 2009), reduced cloud cover in Costa Rican montane forests (Pounds et al. 1999), and the possibility of severe droughts in lowland Amazon forests (Phillips et al. 2009).

How to reconcile these and similar broad trends with the modern-day tropical forest N cycle is unclear. Although empirical observations are limited, the widespread tendency for tropical forests to leak bioavailable N suggests that any governing mechanism(s) ought to operate at a synoptic scale.

SYNTHESIS: THE LEAKY NITROSTAT MODEL

We propose a conceptual model capable of resolving the paradox of tropical N richness at levels of both ecosystem and individual physiology. Our model depends on the interaction of several factors that determine N inputs to tropical forests. First we assume based on theory and observations that symbiotic N-fixing trees employ a perfectly facultative strategy. These fixers can therefore selfishly induce N fixation in any N-poor environment created by disturbances such as soil erosion, tree blowdown, fire, or flooding. Such up-regulation of N inputs is not limited to young trees, as evidenced by nodulation by adults in the litter layer of Cameroon forests (Sprent 2001) and in tree fall gaps of Panamanian forests (Barron 2007). In N-rich conditions, however, trees appear to down-regulate fixation to low or negligible levels—a strategy that benefits the individual by minimizing energetic costs. Functionally, N-fixing trees can therefore act to rapidly redress any local N deficiencies that develop within tropical landscapes in the manner of a nitrostat (Menge &

Hedin 2009), but are not capable of elevating N above P or other resources in the manner shown in **Figure 2b**.

Second, we assume that N bioavailability is not homogeneously distributed within forests, but that there exist localized biogeochemical niches in which N fixers are decoupled from N conditions in soils (Menge & Hedin 2009). Of central importance is the existence of vertical gradients in N fixation (Barron et al. 2009, Menge & Hedin 2009, Reed et al. 2008), which imply that some layers can remain N poor even though others are N rich. For example, the soil litter layer is naturally N poor because plant tissues are rich in C relative to N compared to decomposers. Sustained litterfall ensures that this layer remains N poor and that it immobilizes bioavailable N. The litter layer therefore remains an environment in which heterotrophic bacteria (and possibly shallow-rooted plants) can gain individual benefit through N fixation, even if deeper soils are N rich and produce bioavailable N by mineralization. The canopy layer can be analogously treated as N poor assuming that epiphytic fixers are largely decoupled from soil N conditions (Menge & Hedin 2009).

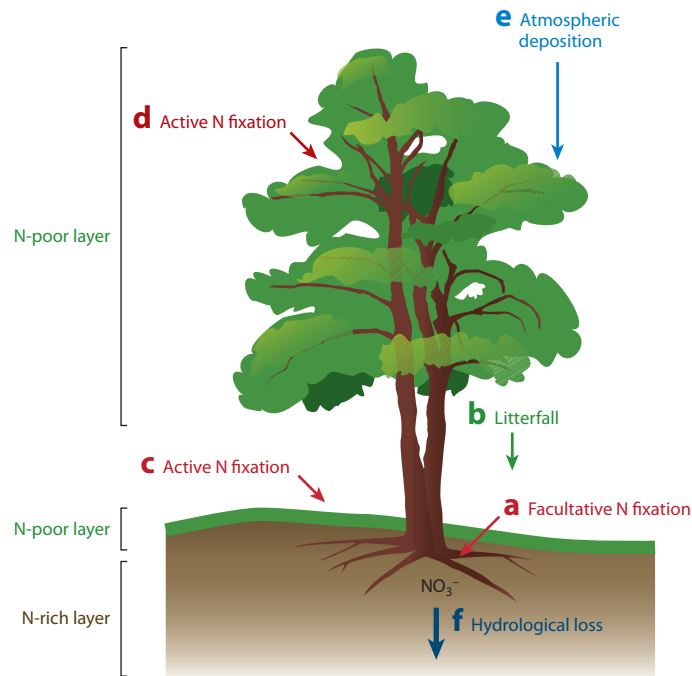


Figure 4

The leaky nitrostat model. We propose this conceptual model capable of resolving the paradox of tropical N richness at both levels of the ecosystem and individual organisms. In N-rich conditions, nitrate accumulates in soils causing facultative N-fixing legume trees (*a*) to cease N fixation and, thus, act as a nitrostat *sensu* Menge & Hedin (2009). However, the process of annual litterfall (*b*) generates a thin layer of litter and organic soil on the soil surface, which remains N poor and can sustain active N fixation by heterotrophic bacteria (or possibly shallowly rooted legumes) (*c*). Similarly, the forest canopy can be considered independent of soil N availability such that it remains N poor even if soil nitrate builds up. The canopy can thus sustain active N fixation. (*d*) External N also enters the system via atmospheric deposition. (*e*) Ecosystem N inputs by nonlegume fixation and deposition combined (*c* + *d* + *e*) are large enough to maintain N richness over other resources in deeper soil layers and to sustain hydrological losses of nitrate to groundwater and watershed streams (*f*).

Third, we assume that despite the lack of active fixation by trees in N-rich conditions, significant amounts of N enter the ecosystem through three vectors that each function independent of soil N conditions: heterotrophic fixation in litter of shallow soils (vector c in **Figure 4**), canopy fixation by epiphytic fixers (vector d), and atmospheric N deposition (vector e). In combination, these three vectors are, in many forests, capable of delivering sufficient amounts of N to further up-regulate the N cycle beyond other resources and to generate a sustained leak of bioavailable N from the nitrostat.

The N paradox considered here offers a prime example of lack of parsimony between explanations at ecosystem versus individual levels of biological organization. Our model offers the essential dynamics needed to generate and sustain richness in N relative to P and other resources in humid tropical forests. Our explanation depends on the existence of heterogeneity within ecosystem pools traditionally considered fully mixed and defined by a single mean field condition. Although the model assumes a vertical gradient in N availability, it does not at this point seek to explain remaining issues of horizontal or vertical redistribution of N or other resources. Such redistribution occurs through litterfall, root turnover, or mycorrhizal symbioses and may have local implications for strategies of N fixation among organisms. Indeed, the paradox of tropical N richness identifies the need to integrate organismal and ecosystem approaches to resolve fundamental issues of how our Earth system is organized.

FUTURE ISSUES

1. Resolution of the tropical N cycle is critical because it affects our understanding of how tropical forests function within the integrated Earth-climate system.
2. We lack basic information about the tropical forest N cycle and how it varies in space and time. Of particular concern is N fixation by legumes and nonlegumes and the role of atmospheric, hydrologic, and gaseous vectors in determining forest N balances.
3. There is great need to understand the ecology and evolution of strategies of N fixation among tropical trees and how these strategies impact tropical nutrient cycles.
4. We know little about the dependency of N fixation on the macronutrients N and P or micronutrients such as molybdenum, iron, or vanadium.

DISCLOSURE STATEMENT

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

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LITERATURE CITED

Aber JD, McDowell WH, Nadelhoffer KJ, Magill A, Berntson G, et al. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. *BioScience* 48:921–34

- Barron AR. 2007. *Patterns and controls on nitrogen fixation in a lowland tropical forest, Panama*. PhD thesis. Princeton Univ.
- Barron AR, Wurzburger N, Bellenger JP, Wright SJ, Hedin LO. 2009. Molybdenum limitation of asymbiotic nitrogen fixation in tropical forest soils. *Nat. Geosci.* 2(1):42–45
- Beirnaert A. 1941. La technique culturale dans l'Equateur. Influence de la culture sur les reserves en humus et en azote des terres equatoriales. *Publ. Inst. Natl. Agron. Congo Belge (INEAC) Ser. Tech.* 26:1–86
- Benner JW, Concroy S, Lunch CK, Toyoda N, Vitousek PM. 2007. Phosphorus fertilization increases the abundance and nitrogenase activity of the cyanolichen *Pseudocyphellaria crocata* in Hawaiian montane forests. *Biotropica* 39:400–05
- Benner JW, Vitousek PM. 2007. Development of a diverse epiphyte community in response to phosphorus fertilization. *Ecol. Lett.* 10:628–36
- Biggs TW, Dunne T, Martinelli LA. 2004. Natural controls and human impacts on stream nutrient concentrations in a deforested region of the Brazilian Amazon basin. *Biogeochemistry* 68:227–57
- Binkley D, Sollins P, Bell R, Sachs D, Myrold D. 1992. Biogeochemistry of adjacent conifer and alder–conifer stands. *Ecology* 73:2022–33
- Boddey RM, Peoples MB, Palmer B, Dart PJ. 2000. Use of the N15 natural abundance technique to quantify biological nitrogen fixation by woody perennials. *Nutr. Cycl. Agroecosyst.* 57:235–70
- Bonan GB. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–49
- Bonnier C. 1958. Discussion: Chapter 13: some factors affecting nodulation in the tropics, by GB Masefield. In *Nutrition of the Legumes*, ed. EG Hallsworth, pp. 212–13. London: Butterworths
- Bordeleau LM, Prévost D. 1994. Nodulation and nitrogen fixation in extreme environments. *Plant Soil* 161:115–25
- Boy J, Rollenbeck R, Valarezo C, Wilcke W. 2008. Amazonian biomass burning-derived acid and nutrient deposition in the north Andean montane forest of Ecuador. *Glob. Biogeochem. Cycles* 22(4):GB4011
- Brown S, Lugo EA. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14:161–87
- Chave J, Condit R, Muller-Landau HC, Thomas SC, Ashton PS, et al. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biol.* 6:e45
- Cleveland CC, Steven AR, Schmidt K. 2002. Phosphorus limitation of microbial processes in moist tropical forests: evidence from short-term laboratory incubations and field studies. *Ecosystems* 5(7):680–91
- Cleveland CC, Townsend AR, Schimel DS, Fisher H, Howarth RWH, et al. 1999. Global patterns of terrestrial biological nitrogen (N₂) fixation in natural ecosystems. *Glob. Biogeochem. Cycles* 13(2):623–45
- Crews TE. 1999. The presence of nitrogen fixing legumes in terrestrial communities: Evolutionary vs ecological considerations. *Biogeochemistry* 46(1–3):233–46
- Crews TE, Farrington H, Vitousek PM. 2000. Changes in asymbiotic heterotrophic nitrogen fixation on leaf litter of *Metrosideros polymorpha* with long-term ecosystem development in Hawaii. *Ecosystems* 3:386–95
- Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, et al. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76:1407–24
- Daufresne T, Hedin LO. 2005. Plant coexistence depends on ecosystem nutrient cycles: extension of the resource-ratio theory. *Proc. Natl. Acad. Sci. USA* 102:9212–17
- Davidson EA, de Carvalho CJR, Vieira ICG, Figueiredo RO, Moutinho P, et al. 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecol. Appl.* 14(4):S150–63
- Davidson EA, Reis de Carvalho CJ, Figueira AM, Ishida FY, Ometto JPHB, et al. 2007. Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447:995–98
- de Faria SM, de Lima HC. 1998. Additional studies of the nodulation status of legume species in Brazil. *Plant Soil.* 200:185–92
- de Faria SM, Lewis GP, Sprent JI, Sutherland JM. 1989. Occurrence of nodulation in the leguminosae. *New Phytol.* 111:607–19
- Dentener F, Drevet J, Lamarque JF, Bey I, Eickout B, et al. 2006. Nitrogen and sulfur deposition on regional and global scales: a multimodel evaluation. *Glob. Biogeochem. Cycles* 20:GB4003
- Evans RD. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends Plant. Sci.* 6:121–26

- Ewel JJ. 1976. Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *J. Ecol.* 64:293–308
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–40
- Fittkau EJ. 1971. Esboço de uma divisão ecológica da região amazônica. *Proc. Symp. Biol. Trop. Amaz., Florencia Letícia 1969*, pp. 363–72
- Forti CM, Melfi AJ, Astolfo R, Fostier A-H. 2000. Rainfall chemistry composition in two ecosystems in the northeastern Brazilian Amazon (Amapá State). *J. Geophys. Res.* 105(D23):28895–905
- Fox RL, de la Pena RS, Gavenda RT, Habte M, Hue NV, et al. 1991. Amelioration, revegetation, and subsequent soil formation in denuded bauxitic materials. *Allertonia* 6(2):128–84
- Freiberg E. 1998. Microclimatic parameters influencing nitrogen fixation in the phyllosphere of a Costa Rican premontane rain forest. *Oecologia* 17:9–18
- Fyllas NM, Patiño S, Baker TR, Bielefeld Nardoto G, Martinelli LA, et al. 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosci. Discuss.* 6:3707–69
- Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, et al. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70:153–226
- Galloway JN, Schlesinger WH, Levy H, Michaels A, Schnoor JL. 1995. Nitrogen fixation: anthropogenic enhancement–environmental response. *Glob. Biogeochem. Cycles* 9:235–52
- Gerber S, Hedin LO, Oppenheimer M, Pacala SW, Shevliakova E. 2009. Nitrogen cycling and feedbacks in a global dynamic land model. *Glob. Biogeochem. Cycles* In press (doi: 10.1029/2008GB003336)
- Greenland DJ, Kowal JM. 1960. Nutrient content of the moist tropical forest of Ghana. *Plant Soil* 12(2):154–74
- Grubb PJ. 1977. Control of forest growth and distribution on wet tropical mountains—with special reference to mineral nutrition. *Annu. Rev. Ecol. Syst.* 8:83–107
- Grubb PJ. 1989. Mineral nutrients: a plant ecologist's view. In *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*, ed. J Proctor, pp. 417–39. Oxford, UK: Blackwell
- Gutschick VP. 1981. Evolved strategies in nitrogen acquisition by plants. *Am. Nat.* 118(5):607–37
- Hall SJ, Matson PA. 1999. Nitrogen oxide emissions after nitrogen additions in tropical forests. *Nature* 400:152–55
- Harrington RA, Fownes JH, Vitousek PM. 2001. Production and resource use efficiencies in N- and P-limited tropical forests: a comparison of responses to long-term fertilization. *Ecosystems* 4(7):646–57
- Hartwig UA. 1998. The regulation of symbiotic N₂ fixation: a conceptual model of N feedback from the ecosystem to the gene expression level. *Perspect. Plant Ecol. Evol. Syst.* 1:92–120
- Haug GH, Hughen KA, Sigman DM, Peterson LC, Röhl U. 2001. Southward migration of the intertropical convergence zone through the Holocene. *Science* 239:1304–8
- Hedin LO. 2004. Global organization of terrestrial plant–nutrient interactions. *Proc. Natl. Acad. Sci. USA* 101(30):10849–50
- Hedin LO, Armesto JJ, Johnson AH. 1995. Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. *Ecology* 76(2):493–509
- Hedin LO, Vitousek PM, Matson PA. 2003. Nutrient losses over four million years of tropical forest development. *Ecology* 84:2231–55
- Hemp A. 2009. Climate change and its impact on the forests of Kilimanjaro. *Afr. J. Ecol.* 47:3–10
- Herbert DA, Fownes JH. 1995. Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. *Biogeochemistry* 29:223–35
- Herrera R, Jordan CF, Klinge H, Medina E. 1978. Amazon ecosystems—their structure and functioning with particular emphasis on nutrients. *Interciencia* 3(4):223–32
- Högberg P. 1997. N-15 natural abundance in soil–plant systems. Tansley Review No. 95. *New Phytol.* 137(2):179–203
- Högberg P. 1986. Soil nutrient availability, root symbioses and tree species composition in tropical Africa: a review. *J. Trop. Ecol.* 2:359–72
- Houlton BZ, Sigman DM, Hedin LO. 2006. Isotopic evidence for large gaseous nitrogen losses from tropical rainforests. *Proc. Natl. Acad. Sci. USA* 103(23):8745–50
- Houlton BZ, Sigman DM, Schuur EAG, Hedin LO. 2007. A climate-driven switch in plant nitrogen acquisition within tropical forest communities. *Proc. Natl. Acad. Sci. USA* 104(21):8902–6

- Houlton BZ, Wang Y-P, Vitousek PM, Field CB. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454:327–30
- Ingestad T. 1980. Growth, nutrition, and nitrogen fixation in gray alder at varied rate of nitrogen addition. *Physiol. Plant.* 50:353–64
- Jenny H. 1950. Causes of the high nitrogen and organic matter content of certain tropical forest soils. *Soil Sci.* 69(1):63–69
- Jenny H, Bingham FT, Padilla-Saravia B. 1948. Nitrogen and organic matter contents of equatorial soils of Colombia, South America. *Soil Sci.* 66:173–86
- Jenny H, Gessel SP, Bingham FT. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Sci.* 68:419–32
- Kaspari M, Garcia MN, Harms KE, Santana M, Wright SJ, Yavitt JB. 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecol. Lett.* 11:35–43
- Keay RWJ. 1953. *An Outline of Nigerian Vegetation*. Lagos, Nigeria: Gov. Printer. 2nd ed.
- Kitayama K, Aiba SI. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *J. Ecol.* 90(1):37–51
- LeBauer DS, Treseder KK. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89:371–79
- Lesack LFW. 1993. Export of nutrients and major ionic solutes from a forest catchment in the central Amazon Basin. *Water Resour. Res.* 29:743–75
- Lewis SL, Lopez-Gonzalez G, Sonke B, Affum-Baffoe K, Baker TR, et al. 2009. Increasing carbon storage in intact African tropical forests. *Nature* 457:1003–7
- Lewis WM Jr, Melack JM, McDowell WH, McClain M, Richey JE. 1999. Nitrogen yields from undisturbed watersheds in the Americas. *Biogeochemistry* 46:149–62
- Losos EC, Leigh EG, eds. 2004. *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. Chicago: Univ. Chicago Press
- Malhi Y, Phillips OL. 2004. Tropical forests and global atmospheric change: a synthesis. *Philos. Trans. R. Soc. London Ser. B* 359:549–55
- Markewitz D, Resende JCF, Parron L, Bustamante M, Klink CA, et al. 2006. Dissolved rainfall inputs and streamwater outputs in an undisturbed watershed on highly weathered soils in the Brazilian cerrado. *Hydrol. Process.* 20:2615–39
- Martinelli LA, Piccolo MC, Townsend AR, Vitousek PM, Cuevas E, et al. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. *Biogeochemistry* 46:45–65
- Matson PA, Vitousek PM. 1987. Cross-system comparison of soil nitrogen transformations and nitrous oxide fluxes in tropical forests. *Glob. Biogeochem. Cycles* 1:163–70
- Matzek V, Vitousek P. 2003. Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rain forest. *Biotropica* 35:12–19
- McDowell WH, Asbury CE. 1994. Export of carbon, nitrogen and major ions from three tropical montane watersheds. *Limnol. Oceanogr.* 39:111–25
- McGroddy ME, Baisden WT, Hedin LO. 2008. Stoichiometry of hydrological C, N, and P losses across climate and geology: an environmental matrix approach across New Zealand primary forests. *Glob. Biogeochem. Cycles* 22(1):GB1026
- McGroddy ME, Daufresne T, Hedin LO. 2004. Scaling of C:N:P stoichiometry in forest worldwide: implications of terrestrial Redfield-type ratios. *Ecology* 85(9):2390–401
- McHargue LA. 1999. *Factors affecting the nodulation and growth of tropical woody legume seedlings*. PhD thesis. Fla. Int. Univ., Miami. 191 pp.
- McKey D. 1994. Legumes and nitrogen: the evolutionary ecology of a nitrogen-demanding lifestyle. In *Advances in Legume Systematics, Part 5: The Nitrogen Factor*, ed. JI Sprent, D McKey, pp. 211–28. Kew, UK: R. Bot. Gard.
- Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL. 1993. Global climate change and terrestrial net primary production. *Nature* 363:234–40
- Menge DNL, Hedin LO. 2009. Nitrogen fixation in different biogeochemical niches along a 120,000-year chronosequence in New Zealand. *Ecology* 90:2190–201

- Menge DNL, Levin SA, Hedin LO. 2008. Evolutionary tradeoffs can select against nitrogen fixation and thereby maintain nitrogen limitation. *Proc. Natl. Acad. Sci. USA* 105:1573–78
- Menge DNL, Levin SA, Hedin LO. 2009a. Facultative versus obligate nitrogen fixation strategies and their ecosystem consequences. *Am. Nat.* In press
- Menge DNL, Pacala SW, Hedin LO. 2009b. Emergence and maintenance of nutrient limitation over multiple time scales in terrestrial ecosystems. *Am. Nat.* 173:164–75
- Mirmanto E, Proctor J, Green J, Nagy L, Suriantata. 1999. Effects of nitrogen and phosphorus fertilization in lowland evergreen rainforest. *Philos. Trans. R. Soc. London Ser. B* 354:1825–29
- Moreira FMS, Da Silva MF, de Faria SM. 1992. Occurrence of nodulation in legume species in the Amazon region of Brazil. *New Phytol.* 121:563–70
- Moreira FMS, Franco AA. 1994. Rhizobia-host interactions in tropical ecosystems in Brazil. In *Advances in Legume Systematics, Part 5: The Nitrogen Factor*, ed. JI Sprent, D McKey, pp. 63–74. Kew, UK: R. Bot. Gard.
- Nardoto GB, Ometto JPHB, Ehleringer JR, Bastamante MMC, Martinelli LA. 2008. Understanding the influences of spatial patterns on N availability within the Brazilian Amazon Forest. *J. Ecosyst.* 11(8):1234–46
- Neff JC, Chapin FS, Vitousek PM. 2004. Breaks in the cycle: dissolved organic nitrogen in terrestrial ecosystems. *Front. Ecol. Environ.* 1(4):205–11
- Neill C, Deegan LA, Thomas SM, Cerri CC. 2001. Deforestation for pasture alters nitrogen and phosphorus in soil solution and streamwater of small Amazonian watersheds. *Ecol. Appl.* 11:1817–28
- Newbery DM, Chuyong GB, Green JJ, Songwe NC, Tchuenteu F, Zimmermann L. 2002. Does low phosphorus supply limit seeding establishment and tree growth in groves of ectomycorrhizal trees in a central African rainforest. *New Phytol.* 156:297–311
- Newbold JD, Sweeney BW, Jackson JK, Kaplan LA. 1995. Concentrations and export of solutes from six mountain streams in northwestern Costa Rica. *J. North Am. Benthol. Soc.* 14:21–37
- Norris DO. 1969. Observations on the nodulation status of rainforest leguminous species in Amazonia and Guyana. *Trop. Agric.* 46:145–51
- Nye PH. 1961. Organic matter and nutrient cycles under moist tropical forest. *Plant Soil.* 13:333–46
- Olsen FJ, Hamilton G, Elkins DM. 1975. Effect of nitrogen on nodulation and yield of soybean. *Exp. Agric.* 11:289–94
- Pate JS, Dart PJ. 1961. Nodulation studies in legumes IV The influence on inoculum strain and time of application of ammonium nitrate on symbiotic response. *Plant Soil* 15:329–46
- Pearson HL, Vitousek PM. 2001. Stand dynamics, nitrogen accumulations, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. *Ecol. Appl.* 11:1381–94
- Perakis SS, Hedin LO. 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415:416–19
- Phillips OL, Aragão LE, Lewis SL, Fisher JB, Lloyd JL, et al. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323:1344–47
- Phillips OL, Malhi Y, Higuchi N, Laurance WF, Nunez PV, et al. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–42
- Pons TL, Perreijn K, van Kessel C, Weger MJA. 2006. Symbiotic nitrogen fixation in a tropical rainforest: ¹⁵N natural abundance measurements supported by experimental isotopic enrichment. *New Phytol.* 173:154–67
- Porder S, Vitousek PM, Chadwick OA, Chamberlain CP, Hiley GE. 2007. Uplift, erosion, and phosphorus limitation in terrestrial ecosystems. *Ecosystems* 10(1):158–70
- Post WM, Pastor J. 1985. Global patterns of soil storage. *Nature* 317:613–16
- Pounds JA, Fogden MPL, Campbell JH. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611–15
- Pringle CM, Triska FJ, Browder G. 1990. Spatial variation in basic chemistry of streams draining a volcanic landscape on Costa Rica's Caribbean slope. *Hydrobiologia* 206:73–85
- Quesada CA, Lloyd J, Anderson LO, Fyllas NM, Schwarz M, et al. 2009. Soils of Amazonia with particular reference to the rainforest sites. *Biogeosci. Discuss.* 6:3851–392

- Ramos-Escobedo MG, Vazquez G. 2001. Major ions, nutrients and primary productivity in volcanic neotropical streams draining rainforest and pasture catchments at Los Tuxtlas, Veracruz, Mexico. *Hydrobiologia* 445:67–76
- Redfield AC. 1958. The biological control of chemical factors in the environment. *Am. Sci.* 46:205–21
- Reed SC, Cleveland CC, Townsend AR. 2007. Controls over leaf litter and soil nitrogen fixation in two lowland tropical rain forests. *Biotropica* 39(5):585–92
- Reed SC, Cleveland CC, Townsend AR. 2008. Tree species control rates of free-living nitrogen fixation in a tropical rain forest. *Ecology* 89(10):2924–34
- Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci. USA* 101(30):11001–6
- Richardson SJ, Allen RB, Doherty JE. 2008. Shifts in leaf N:P ratio during resorption reflect soil P in temperate rainforest. *Funct. Ecol.* 22(4):738–45
- Richter DD, Babbar LI. 1991. Soil diversity in the tropics. *Adv. Ecol. Res.* 21:315–89
- Robertson GP, Rosswall T. 1986. Nitrogen in west Africa: the regional cycle. *Ecol. Monogr.* 56:43–72
- Robertson GP, Tiedje JM. 1988. Deforestation alters denitrification in a lowland tropical rain forest. *Nature* 336:756–59
- Roggy JC, Prevost MF, Gourbiere F, Casabianca H, Garbaye J, et al. 1999. Leaf natural N-15 abundance and total N concentration as potential indicators of plant N nutrition in legumes and pioneer species in a rain forest of French Guiana. *Oecologia* 120(2):171–82
- Sanchez P. 1976. *Properties and Management of Soils in the Tropics*. New York: Wiley
- Santiago LS, Schuur EAG, Silvera K. 2005. Nutrient cycling and plant-soil feedbacks along a precipitation gradient in lowland Panama. *J. Trop. Ecol.* 21:461–70
- Saur E, Carcelle S, Guezennec S, Rousteau A. 2000. Nodulation of legume species in wetlands of Guadeloupe (Lesser Antilles). *Wetlands* 20:730–34
- Schrumpf M, Zech W, Axmacher JC, Lyaruu HVM. 2006. Biogeochemistry of an afro-tropical montane rain forest on Mt. Kilimanjaro, Tanzania. *J. Trop. Ecol.* 22:77–89
- Silver WL. 1994. Is nutrient availability related to plant nutrient use in humid tropical forests. *Oecologia* 98:336–43
- Sprent JI. 2001. *Nodulation in Legumes*. Kew, UK: R. Bot. Gard.
- Sprent JI. 2005. Nodulated legume trees. In *Nitrogen Fixation in Agriculture, Forestry, Ecology and the Environment*, ed. D Werner, WE Newton, pp. 113–41. New York: Springer-Verlag
- Sprent JI. 2009. *Legume Nodulation: Global Perspective*. Oxford: Wiley-Blackwell
- Sprent JI, Sprent P. 1990. *Nitrogen Fixing Organisms*. London, UK: Chapman & Hall
- Sylvester-Bradley R, de Oliveira LA, Filho JAD, St. John TV. 1980. Nodulation of legumes, nitrogenase activity of roots and occurrence of nitrogen-fixing *Azospirillum* spp. in representative soils of central Amazonia. *Agro-Ecosyst.* 6:249–66
- Tanner EVJ, Kapos V, Franco W. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* 73(1):78–86
- Tanner EVJ, Kapos V, Freskos S, Healey JR, Theobald AM. 1990. Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *J. Trop. Ecol.* 6:231–38
- Tanner EVJ, Vitousek PM, Cuevas E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79(1):10–22
- Thompson J, Proctor J, Viana V, Milliken W, Ratter JA, Scott DA. 1992. Ecological studies on a lowland evergreen rain forest on Maraca Island, Roraima, Brazil: I Physical environment, forest structure and leaf chemistry. *J. Ecol.* 80:689–703
- Townsend AR, Asner GP, Cleveland CC. 2008. The biogeochemical heterogeneity of tropical forests. *Trends Ecol. Evol.* 23(8):424–31
- Townsend AR, Cleveland CC, Asner GP, Bustamante MMC. 2007. Controls over foliar N:P ratios in tropical rain forests. *Ecology* 88:107–18
- Van Kessel C, Roskoski JP. 1983. Effect of fertilizers and soil shading on nodulation and nitrogen-fixation (acetylene-reduction) of Inga-jinicuil seedlings. *Plant Soil* 72:95–105
- Van Wambeke A. 1992. *Soils of the Tropics. Their Properties and Appraisal*. New York: McGraw-Hill

- Vitousek PM. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–98
- Vitousek PM, Cassman K, Cleveland C, Crews T, Field CB, et al. 2002. Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry* 57:1–45
- Vitousek PM, Farrington H. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* 37:63–75
- Vitousek PM, Hedin LO, Matson PA, Fownes JH, Neff J. 1998. Within-system element cycles, input-output budgets, and nutrient limitation. *Successes, Limitations, and Frontiers in Ecosystem Science*, ed. ML Pace, PM Groffman, pp. 432–51. New York: Springer-Verlag
- Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13(2):87–115
- Vitousek PM, Matson PA. 1988. Nitrogen transformations in tropical forest soils. *Soil Biol. Biochem.* 20:361–67
- Vitousek PM, Sanford RL Jr. 1986. Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* 17:137–67
- Wardle DA, Walker LR, Bardgett RD. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305:509–13
- Wilcke W, Yasini S, Valarez C, Sech W. 2001. Change in water quality during the passage through a tropical montane rain forest in Ecuador. *Biogeochemistry* 55:45–72
- Williams MR, Fisher TR, Melack JM. 1997. Solute dynamics in soil water and groundwater in a central Amazon catchment undergoing deforestation. *Biogeochemistry* 38:303–35