Large losses of inorganic nitrogen from tropical rainforests suggest a lack of nitrogen limitation

Abstract

Inorganic nitrogen losses from many unpolluted mature tropical forests are over an order of magnitude higher than losses from analogous temperate forests. This pattern could either reflect a lack of N limitation or accelerated plant–soil N cycling under tropical temperatures and moisture. We used a simple analytical framework of the N cycle and compared our predictions with data of N in stream waters of temperate and tropical rainforests. While the pattern could be explained by differences in N limitation, it could not be explained based on up-regulation of the internal N cycle without invoking the unlikely assumption that tropical plants are two to four times less efficient at taking up N than temperate plants. Our results contrast with the idea that a tropical climate promotes and sustains an up-regulated and leaky – but N-limited – internal N cycle. Instead, they are consistent with the notion that many tropical rainforests exist in a state of N saturation.

Keywords

Analytical model, biogeochemical theory, biogeochemistry, climate, nitrogen (N) limitation and cycling, N losses, N saturation, plant–soil cycle, temperate rainforest, tropical rainforest.

INTRODUCTION

Over the last couple of decades, observations have revealed large dissolved and gaseous losses of inorganic nitrogen (N\textsubscript{i}) from seemingly unpolluted mature tropical forests across a range of soil types and ages (Bruijnzeel 1991; McDowell & Ashury 1994; Newbold et al. 1999; Lewis et al. 1999; Hedin et al. 2003, 2009; Houlton et al. 2006). These N\textsubscript{i} losses are over an order of magnitude higher than from their unpolluted temperate counterparts (Hedin et al. 1995; Perakis & Hedin 2002; Vanderbil et al. 2003; McGroddy et al. 2008), and in fact, occur at levels characteristic of highly polluted, N-saturated temperate forests (Aber et al. 1998; Hedin et al. 2009). Are mature, unpolluted tropical rainforests across large parts of the globe N-saturated? Or alternatively, are such high losses consistent with N limitation, but simply the expression of an up-regulated N cycle (including losses) in a hot and wet climate? Arguments for both possibilities can be found in the literature.

Starting with Jenny’s (1950) influential observations, researchers have reported that tropical forests can accumulate and recycle large amounts of N relative to temperate forests (e.g. Vitousek & Sanford 1986), and often harbour an abundance of potentially N fixing tree species (see Table 1 in Hedin et al. (2009) for a recent compilation), a functional group of plants that is virtually absent from late-successional temperate forests (Menge et al. 2010). Such observations have over the last several decades led to the widely cited idea that vast areas of the tropics are not limited by N, but rather by phosphorus (P; Vitousek 1984; Hedin et al. 2009; Cleveland et al. 2011).

At the same time, rates of nutrient recycling between plants and detritus are both faster and more complete (i.e. nutrients are mineralised) in tropical forests due to high temperatures and moisture (Parton et al. 2007) – a condition that might be consistent with high losses of N\textsubscript{i} from the plant–soil cycle which, in turn, might promote N limitation and the existence of plant and microbial mechanisms for efficient nutrient capture. Indeed, part of the lore of tropical forests found frequently in textbook descriptions of the biome is that tropical nutrient cycles – including N – are highly conservative and display uptake and recycling strategies adapted to soils that have been rendered nutrient scarce by long-term leaching (Richards 1973; Jordan et al. 1979; Jordan & Herrera 1981). These different views highlight major uncertainties in the tropical N cycle and climate–nutrient cycling relationships in general.

Nutrient fertilisation studies in the tropics are few, and results are mixed, particularly with regard to late-successional forests (Vitousek & Farrington 1997; Tanner et al. 1998; Kaspari et al. 2008). A recent meta-analysis showed a similar if not higher prevalence of N limitation in tropical forests compared with temperate forests, although that study noted that site selection bias probably played a role in this result (LeBauer & Treseder 2008). Other experimental data, such as those showing large gaseous losses following both long-term and single-application N fertilisation from some Hawaiian sites (Hall & Matson 2003), are consistent with N saturation, but these are also derived from very few sites worldwide.

The large quantity of hydrological loss data from a large diversity of forests worldwide makes it an appealing tool to assess N limitation.
Conceptual models have, for decades, suggested that large N losses indicate N saturation and small N losses indicate N limitation (Vitousek & Reiners 1975; Hedin et al. 1995; Aber et al. 1998; Perakis & Hedin 2002), and simulation models have supported these ideas (Vitousek et al. 1998). Building off these conceptual and simulation models, recent analytical models (Menge et al. 2009b) have provided simple quantitative tools to evaluate what level of losses indicate N limitation versus N saturation, i.e. what constitutes high versus low N.

Our purpose here is to use one of these quantitative tools with globally distributed N loss data to determine the more likely explanation for the wide disparity in N losses observed between tropical and temperate rainforests worldwide. Specifically, we compare two alternative hypotheses to explain the observed differences in N losses between temperate and tropical forests: (1) most forests in both tropical and temperate biomes are N-limited, but climatic effects – a larger, faster-cycling N pool under warmer conditions – lead to higher N losses in tropical forests and (2) most temperate forests are N-limited, but most tropical forests are N-saturated. We evaluate these hypotheses using a model that describes the dynamics of mineral N pools (nitrate and ammonium) in soils. Processes included are external inputs (e.g. atmospheric deposition), net mineralisation, plant uptake and leaching losses. We evaluate N losses under the hypothesis of N limitation, while allowing for parameters sensitive to climate to vary for temperate versus tropical forests. These parameters are N inputs, N mineralisation, plant uptake capacity and soil depth. If these climate-sensitive parameters cannot account for the observed differences in temperate versus tropical rainforest N losses, the hypothesis is falsified, implying that mature tropical rainforests are not generally limited by N.

**MODEL DEVELOPMENT AND ANALYTICAL APPROACH**

Our model consists of a single differential equation that tracks changes in N

$$\frac{dN_i}{dt} = I + M - k_p N_i - k_l N_i$$

The fluxes considered (in units of N mass/soil surface area/time) are external inputs (I) from atmospheric deposition, internal net mineralisation (M) of organic detrital N, plant uptake of N_i (k_p N_i) and leaching loss of N_i (k_l N_i) from the plant-soil system, where k_p and k_l are first order constants of plant uptake and leaching losses (with units

---

**Table 1** Climatic and stream N characteristics of study watersheds

<table>
<thead>
<tr>
<th>Watershed</th>
<th>MAT (°C)</th>
<th>MAP (cm per year)</th>
<th>NO_3 (μg N L⁻¹)</th>
<th>NO_3 (kg N ha⁻¹ year⁻¹)</th>
<th>NH₄⁺ (μg N L⁻¹)</th>
<th>NH₄⁺ (kg N ha⁻¹ year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chiloe, Chile¹</td>
<td>6</td>
<td>584</td>
<td>1</td>
<td>0.05</td>
<td>13</td>
<td>0.7</td>
</tr>
<tr>
<td>Chiloe</td>
<td>6</td>
<td>584</td>
<td>7</td>
<td>0.4</td>
<td>23</td>
<td>1.2</td>
</tr>
<tr>
<td>HJ Andrews, OR²</td>
<td>9</td>
<td>250</td>
<td>1</td>
<td>0.02</td>
<td>7</td>
<td>0.09</td>
</tr>
<tr>
<td>WS8</td>
<td>9</td>
<td>250</td>
<td>3</td>
<td>0.03</td>
<td>8</td>
<td>0.08</td>
</tr>
<tr>
<td>WS8</td>
<td>9</td>
<td>250</td>
<td>4</td>
<td>0.04</td>
<td>2</td>
<td>0.09</td>
</tr>
<tr>
<td>Coweeta, NC³</td>
<td>13</td>
<td>181</td>
<td>5</td>
<td>0.04</td>
<td>2</td>
<td>0.02</td>
</tr>
<tr>
<td>WS2</td>
<td>13</td>
<td>187</td>
<td>7</td>
<td>0.07</td>
<td>3</td>
<td>0.03</td>
</tr>
<tr>
<td>WS18</td>
<td>13</td>
<td>196</td>
<td>5</td>
<td>0.06</td>
<td>3</td>
<td>0.03</td>
</tr>
<tr>
<td>WS27</td>
<td>12</td>
<td>239</td>
<td>2</td>
<td>0.03</td>
<td>4</td>
<td>0.07</td>
</tr>
<tr>
<td>WS32</td>
<td>12</td>
<td>222</td>
<td>3</td>
<td>0.04</td>
<td>4</td>
<td>0.06</td>
</tr>
<tr>
<td>WS34</td>
<td>12</td>
<td>191</td>
<td>4</td>
<td>0.05</td>
<td>3</td>
<td>0.03</td>
</tr>
<tr>
<td>WS36</td>
<td>12</td>
<td>216</td>
<td>10</td>
<td>0.18</td>
<td>3</td>
<td>0.06</td>
</tr>
<tr>
<td>Maimai, NZ⁴</td>
<td>1</td>
<td>260</td>
<td>31</td>
<td>0.48</td>
<td>15</td>
<td>0.2</td>
</tr>
<tr>
<td>2</td>
<td>260</td>
<td>28</td>
<td>0.2</td>
<td>14</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>Olympic NP, WA⁵</td>
<td>1</td>
<td>350</td>
<td>73</td>
<td>2.3</td>
<td>10</td>
<td>0.3</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>10 ± 2</td>
<td>281 ± 110</td>
<td>12 ± 19</td>
<td>0.3 ± 0.6</td>
<td>8 ± 6</td>
<td>0.2 ± 0.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Watershed</th>
<th>MAT (°C)</th>
<th>MAP (cm per year)</th>
<th>NO_3 (μg N L⁻¹)</th>
<th>NO_3 (kg N ha⁻¹ year⁻¹)</th>
<th>NH₄⁺ (μg N L⁻¹)</th>
<th>NH₄⁺ (kg N ha⁻¹ year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tempisquequío</td>
<td>23</td>
<td>275</td>
<td>207</td>
<td>6.1</td>
<td>&lt; 5</td>
<td></td>
</tr>
<tr>
<td>Tempisquequío Sur</td>
<td>23</td>
<td>275</td>
<td>115</td>
<td>4.9</td>
<td>&lt; 5</td>
<td></td>
</tr>
<tr>
<td>Khathia</td>
<td>23</td>
<td>275</td>
<td>181</td>
<td>5.6</td>
<td>&lt; 5</td>
<td></td>
</tr>
<tr>
<td>Marian</td>
<td>23</td>
<td>275</td>
<td>254</td>
<td>4</td>
<td>&lt; 5</td>
<td></td>
</tr>
<tr>
<td>Jobo</td>
<td>23</td>
<td>275</td>
<td>297</td>
<td>4.3</td>
<td>&lt; 5</td>
<td></td>
</tr>
<tr>
<td>Zompopa</td>
<td>23</td>
<td>275</td>
<td>215</td>
<td>6</td>
<td>&lt; 5</td>
<td></td>
</tr>
<tr>
<td>Maui, Hawaii⁷</td>
<td>220</td>
<td>16</td>
<td>220</td>
<td>878</td>
<td>16.2</td>
<td>2.04</td>
</tr>
<tr>
<td>245</td>
<td>16</td>
<td>245</td>
<td>268</td>
<td>5.5</td>
<td>3</td>
<td>0.07</td>
</tr>
<tr>
<td>275</td>
<td>16</td>
<td>275</td>
<td>40</td>
<td>0.9</td>
<td>3</td>
<td>0.07</td>
</tr>
<tr>
<td>335</td>
<td>16</td>
<td>335</td>
<td>60</td>
<td>1.8</td>
<td>6</td>
<td>0.2</td>
</tr>
<tr>
<td>405</td>
<td>16</td>
<td>405</td>
<td>8</td>
<td>0.3</td>
<td>3</td>
<td>0.2</td>
</tr>
<tr>
<td>Puerto Rico⁸</td>
<td>1</td>
<td>23</td>
<td>430</td>
<td>66</td>
<td>2.5</td>
<td>18.0</td>
</tr>
<tr>
<td>2</td>
<td>18</td>
<td>438</td>
<td>54</td>
<td>1.4</td>
<td>12</td>
<td>0.3</td>
</tr>
<tr>
<td>3</td>
<td>25</td>
<td>315</td>
<td>62</td>
<td>0.9</td>
<td>15</td>
<td>0.3</td>
</tr>
<tr>
<td>Brazil⁹</td>
<td>1</td>
<td>26</td>
<td>220</td>
<td>90</td>
<td>1.7</td>
<td>42.0</td>
</tr>
<tr>
<td>2</td>
<td>26</td>
<td>220</td>
<td>111</td>
<td>2.1</td>
<td>44</td>
<td>0.8</td>
</tr>
<tr>
<td>Malaysia¹⁰</td>
<td>1</td>
<td>23</td>
<td>255</td>
<td>700</td>
<td>14</td>
<td>18.0</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>21 ± 4</td>
<td>295 ± 69</td>
<td>212 ± 236</td>
<td>5 ± 4</td>
<td>15 ± 10</td>
<td>0.4 ± 0.3</td>
</tr>
</tbody>
</table>

of $k_p$ and $k_i$ in $t^{-1}$). Equation 1 denotes a donor controlled system, where plant N uptake depends on $N_i$ availability, and thus represents the dynamics of an N-limited system. Herein, we address only the dynamics of the $N_i$ pool, which equilibrates over hours to days for a given level of plant biomass and detrital N (Menge et al. 2009b). This focus means that we do not have to assume steady state of the entire forest ecosystem, which would include more variables and processes. An example of such a larger model, and how it would relate to the model given by eqn 1, is shown in Fig. 1. Inputs to and losses from the mineral N pool (those modelled here) are represented by solid arrows, whereas all other processes are represented by dotted arrows. Similarly, non-modelled pools are represented by dotted boxes. As our focus is on the short timescale of mineral N, processes that do not directly interact with this pool are not considered. For example, nitrogen fixation does not directly interact with the mineral N pool, and so it is represented implicitly here in the mineralisation flux, because that is the first interaction between newly fixed N and the mineral N pool.

To analyse the steady-state dynamics of $N_i$ losses, we only need to assume that no large-scale disturbance has occurred in the days prior to each N loss measurement. On this short timescale, plant biomass and detrital N are approximately constant, and so a single differential equation is sufficient to describe the model. On time scales that span forest succession, plant N uptake and growth would also depend on plant biomass, but because plant biomass is a constant on this short timescale, it is included in $k_p$.

As we are interested in understanding controls over $N_i$ losses from mature forests, we do not consider transient losses in the hours to days following disturbance, but rather evaluate the model under quasi-equilibrium conditions in which $dN_i/dt \approx 0$. We thus take advantage of natural time-scale separation for terrestrial N cycles (Menge et al. 2009b) and solve for the quasi equilibrium, by assuming that slower parts of the N cycle (soil organic matter and plant biomass) are constant relative to $N_i$, which equilibrates rapidly and is our focus. Furthermore, in most N-limited cases, the sink strength from plant uptake is much greater than gravity-based losses via dissolved hydrological vectors (i.e. $k_p >> k_i$). That is, we expect an N-limited system to be efficient in retaining available N, and allow very little N to be leached via hydrological pathways. We can therefore solve for the quasi equilibrium of N under N limitation ($\bar{N}_i$, from $dN_i/dt = 0$):

$$\bar{N}_i = \frac{I + M}{k_p + k_i} \approx \frac{I + M}{k_p} \tag{2}$$

Alternatively, under plant N saturation, plants would take up a fixed amount of N depending on their N demand ($U$), and irrespective of N availability. In that case, the steady state would be

$$\bar{N}_i = \frac{I + M - U}{k_i} \tag{3}$$

where $U$ is the plant uptake rate (in N mass area$^{-1}$ t$^{-1}$). Note that saturation also implies $I + M > U$.

To use this model to compare stream $N_i$ concentrations, we need to convert from soil N abundance (in mass N/soil surface area) to stream N (in concentration, i.e., mass N/stream water volume). First, we convert from soil N abundance to soil N concentration (mass N/soil volume) using the active soil depth $h$ $[N_{soil}] = N/h$. To obtain stream N concentrations, we use the empirically supported theoretical result that stream and soil N concentrations are equivalent ($[N]_{stream} = [N]_{soil}$) as long as stream organism biomass is near steady state (Brookshire et al. 2009). Remembering that $k_i << k_p$ (i.e. that in most N-limited cases the sink strength from plant uptake is much greater than gravitational pull), it is straightforward to solve for the exact and approximated N-limited stream $N_i$ concentrations $[N_i]_{L,i}$ (‘L’ for limited) at quasi steady state using the above relationships and eqn 2:

$$[\bar{N}_i]_L = \frac{I + M}{h(k_p + k_i)} \approx \frac{I + M}{hk_p} \tag{4}$$

Similarly, we can approximate the N-saturated case (‘S’ for saturated) of stream $N_i$ concentration as

$$[\bar{N}_i]_S = \frac{I + M - U}{hk_i} \tag{5}$$

To evaluate whether observed differences in temperate and tropical stream $N_i$ concentrations are consistent with N limitation, we examine the ratio of eqn 4 evaluated for the two biomes. This yields

$$\frac{[\bar{N}_i]_{Trop}}{[\bar{N}_i]_{Temp}} \approx \frac{(I + M)_{Trop}}{b \cdot k_p} \frac{(I + M)_{Temp}}{b \cdot k_p} \tag{6}$$

Eqn 6 says that if both biomes are N-limited, the tropical to temperate ratio of stream N concentrations must be explained by tropical forests having higher external inputs, higher net N mineralisation (it is the sum of these two that matters), shallower soils or poorer plant N uptake abilities in comparison with temperate forests. Importantly, although it is informative to have numbers for each of the parameters in each biome, it is only essential to know the relative values across biomes, i.e. the parameter ratios.

We do not parameterise the ratio for the case of N-saturated tropical (eqn 5) and N-limited temperate (eqn 4) forests, because it is
difficult to constrain $U$ with data. However, we note that a wide range of ratios — including a very high tropical to temperate $N_2$ ratio — are plausible because $I + M$ may be close to or much greater than $U$ in an N-saturated scenario.

Model parameterisation and evaluation

We use published stream N data from unpolluted mature forests receiving $\geq 1500$ mm of rain annually, and for which stream dissolved inorganic N (DIN: nitrate + ammonium) concentrations and hydrological losses have been measured for multiple years (Table 1). Mean annual precipitation in our data set did not differ significantly between biomes, whereas mean annual temperatures were on average $10^\circ C$ higher in tropical vs. temperate forests. We did not include dissolved organic N (DON) or particulate N in our estimates of $M$ due to lack of comprehensive data, but the available data do not suggest significant cross-biome differences (e.g. Hedin et al. 1995, 2003; Perakis & Hedin 2002; Houlton et al. 2006; McGroddy et al. 2008).

As global datasets of N mineralisation ($M$) are sparse, we approximated $M$ as litterfall N plus asymbiotic biological N fixation (BNF, which adds N directly to litter and soil organic N pools), which should be a reasonable assumption for mature forests with internal N cycles near equilibrium. We justify this approximation based on global observations of increasing N release from decomposing litter with increasing N content (Parton et al. 2007), strong global relationships between mineralisation and nitrification (Booth et al. 2005) and the theoretical expectation that if this were not the case, litter and soil N pools would rapidly accumulate large amounts of N (which they do not). For litterfall N fluxes, we used global syntheses for mature tropical (Vitousek 1984) and temperate forests (Vogt et al. 1986; Appendix S1), again selecting moist forests with $\geq 1500$ mm annual rainfall. For asymbiotic BNF inputs, we use mean fixation rates for temperate forests and tropical evergreen forests reported by Reed et al. (2011). We do not explicitly consider external inputs from symbiotic BNF, because unlike asymbiotic BNF, these N inputs are fed directly into plant biomass (Fig. 1), and are thus accounted for in the litterfall-mineralisation pathway.

To compare external N sources, we used estimates of atmospheric deposition inferred from global datasets (Dentener et al. 2006). We expect that knowledge of $I$ is less critical than $M$, because in many forests, mineralisation rates exceed $I$ by several times (Gerber et al. 2010).

In estimating the soil depth parameter, $b$, we focus here on the biologically active zone where the bulk of mineralisation and plant uptake occur. A suitable value should thus be the plant rooting depth (as opposed to weathering depth that can be vast in some tropical soils; Eissenbeer 2001). Although there is tremendous variation in soil types and ages found across the tropics globally (Vitousek & Sanford 1986; Townsend et al. 2008; Hedin et al. 2009; Cleveland et al. 2011), global syntheses of fine rooting depths show minimal differences between tropical and temperate forests (Schenk & Jackson 2002). Herein, we used global estimates of 95% fine rooting depths reported for humid tropical and temperate forests (Schenk & Jackson 2002).

This leaves the parameter plant uptake ($k_p$), which is an indicator of the ability of plants to draw down levels of mineral N, and thus indicates the tightness of the internal plant-soil N cycle. Given that root characteristics (e.g. root mass, surface area and length) are similar in the two biomes (Schenk & Jackson 2002), but cycling is faster in the warm tropics, we suspect that $k_p$ is as large as large in the tropics as in temperate forests, but we have no hard data. Therefore, we leave $k_p$ as the lone free parameter in our model. That is, we will use the other information to determine how large the $k_p$ ratio must be in tropical and temperate forests to meet the model assumptions. However, we consider tropical to temperate $k_p$ ratios significantly less than one to be unrealistic because of similar rooting characteristics between temperate and tropical forests. In other words, if $k_p$ must be much lower in tropical than temperate forests to obtain the observed ratio in eqn 6, we would reject the hypothesis that both biomes are N-limited.

We evaluated the likelihood that large interbiome differences in N losses result from climate-scaled internal N cycling in four ways. First, we compared log-transformed differences in observed N losses between temperate ($n = 15$) and tropical ($n = 17$) forests (Table 1) assuming no climate (i.e. biome) effects on any parameter. Second, we up-scaled temperate DIN losses for climate effects on soil depth. Third, we up-scaled temperate DIN losses for biome differences in litterfall (which incorporates effects of symbiotic BNF), asymbiotic BNF and atmospheric deposition. Fourth, we combined variation in rooting depth and $I + M$. The factors we used to upscale effects of $I + M$ and $b$ were derived from eqn 6. We accounted for error in biome means in $I + M$ with quadratic error propagation. Our error propagation for the $I + M$ term accounts for variability in the temperate ($n = 32$) and tropical ($n = 42$) litterfall data (Appendix S1), N deposition and asymbiotic BNF. We assume conservative ranges in deposition (0–8 or 0–9 kg N ha$^{-1}$ year$^{-1}$ for temperate and tropical forests, respectively), which are equivalent to twice the means for each biome in Dentener et al. (2006) and asymbiotic BNF (0–6 and 0–30 kg N ha$^{-1}$ year$^{-1}$ for temperate and tropical forests, respectively, which are equivalent to half the reported range for each biome in Reed et al. 2011). We tested for differences in DIN losses between biomes using Welch’s $t$ test on log-transformed data.

RESULTS

DIN losses vary by a factor of 10 (5.8–17, 95% confidence interval) between our temperate and tropical forests (Fig. 2; Table 1). To be consistent with N limitation according to our model, these differences must reflect similarly large differences arising from some combination of the tropics having higher mineralisation ($M$) plus external input ($I$), lower plant N uptake capacity ($k_p$) and shallower active soil depth ($b$) according to eqn 6. Litterfall N fluxes in our data set average c. 25 kg N ha$^{-1}$ year$^{-1}$ in temperate forests and c. 92 kg N ha$^{-1}$ year$^{-1}$ in tropical forests (Appendix S1). Asymbiotic BNF averages 1.7 kg N ha$^{-1}$ year$^{-1}$ in temperate forests and 7.8 kg N ha$^{-1}$ year$^{-1}$ in tropical forests (Reed et al. 2011). Atmospheric N inputs ($I$) average c. 4 kg N ha$^{-1}$ year$^{-1}$ in our temperate forests and c. 4.5 kg N ha$^{-1}$ year$^{-1}$ in our tropical forests (Dentener et al. 2006). Putting these together, the ($I + M$) ratio in eqn 6 is c. 3.4-fold higher (range 2.6–4.4) in tropical than in temperate forests. We found that climate-scaled DIN concentrations remained significantly ($P < 0.001$, Welch’s $t$ lower than observed tropical DIN concentrations after accounting for differences in litterfall N, deposition and BNF, despite the large variability in both temperate and tropical litterfall and N loss data. Therefore, these differences in N cycling rates alone cannot explain the 10-fold cross-biome difference in DIN leaching losses, as shown in Fig. 2.

The characteristic rooting depth is similar between humid tropical (93 cm) and temperate (112.5 cm) forests (Schenk & Jackson 2002),
suggesting similar values of the size of the active soil layer (β).
Incorporating this 1.2-fold difference shows that the combination of climatic effects on soil depth and mineralisation (including BNF) plus deposition also cannot explain the DIN loss disparity. This leaves the plant N uptake rate, $k_p$, as the lone unknown parameter ratio in eqn 6. To explain the 10 times higher DIN losses in tropical forests under the assumption of N limitation, $k_p$ must be two to four times lower in tropical than in temperate forests to account for the remainder of the difference in DIN losses.

DISCUSSION

According to our analysis, it is unlikely that the 10-fold higher DIN losses from tropical than temperate forests results from differences in rates of plant–soil N cycling alone. Our results suggest that a two- to fourfold difference remains unexplained. This could potentially be caused by differences in plant uptake capacity, a parameter we do not constrain directly. However, given that average plant biomass (and root biomass/surface area) is unlikely to be lower in the tropics (Schenk & Jackson 2002), this would mean a substantially lower affinity for N in a climate that is conducive to faster biological activity, which is hard to reconcile with N limitation. While root densities appear similar across these two large biome types, investment in N uptake may differ. Typically, as N limitation increases, investment in N uptake and thus $k_p$ can be expected to increase as well. Herein, we obtain a much lower N uptake investment in the tropics if we solve eqn 4 for $k_p$, suggesting a transition away from a donor controlled to a saturated system as indicated in eqps 3 and 5. Therefore, our results contrast with the idea that many tropical forests leak comparably large amounts of N due to an up-regulated and leaky – but N-limited – N cycle. Instead, they are consistent with the hypothesis that many mature tropical rainforests worldwide exist in a state of N saturation. This raises the question of how such N richness emerges and is sustained over time.

The idea that plant growth in many tropical forests is not limited by N like in temperate forests, but rather by elements such as P or Ca, is often stated and/or assumed (Hedin et al. 2009). However, evidence has been largely based on indirect measures of foliar and litter fall stoichiometry and observations of ecosystems with highly weathered soils. Furthermore, direct tests of nutrient limitation in mature tropical forests are few, mostly recent, and show variable responses to nutrient fertilisation (Vitousek & Farrington 1997; Tanner et al. 1998; Kaspari et al. 2008; LeBauer & Treseder 2008). In contrast, our analysis is based on the observation that N\textsubscript{i} losses at the ecosystem scale can differ dramatically between forest biomes. Field observations and theoretical analysis have shown that when plant growth is limited by a nutrient or there otherwise exists a strong net sink for that nutrient, losses of available forms of the nutrient at the ecosystem scale should be low (Hedin et al. 1995, 2009; Vitousek et al. 1998; Menge et al. 2009b; Gerber et al. 2010).

Our focus on mature forests allows us to isolate N\textsubscript{i} dynamics at or near equilibrium and thus avoid transient retention associated with net accumulation in vegetation and soils following disturbance. Under this framework, there are only two ways to achieve high loss rates of N\textsubscript{i}; (1) N limitation with a climate-scaled N cycle, which our results do not support and (2) N saturation, which our results do support.

Our main result – that a two- to fourfold difference between tropical and temperate mineral N losses remains unexplained in a purely N-limited model after accounting for climate-dependent differences in litterfall, inputs and rooting depth – is highly significant as is, but two lines of evidence suggest that the two- to fourfold difference might be a substantial underestimate. First, N losses from tropical rainforests may be substantially higher than reported here. Hydrological N losses used in our study (Table 1) are at the low end of losses reported for tropical watersheds summarised previously (Bruijnzeel 1991). We have also simplified our analysis by excluding gaseous losses of N resulting from microbial nitrification and

© 2011 Blackwell Publishing Ltd/CNRS
In fact, there is evidence that the wettest of tropical forests export very little mineral N in stream waters (Houlton et al. 2006), and that gaseous N losses from the terrestrial biosphere are dominated by tropical forests. We suggest then that if denitrification losses originate from the plant-available nitrate pool, underestimation of mineral N losses by our model would be even greater in the tropics, and thus our conclusion that climate alone cannot account for tropical N losses is even stronger.

Second, mean levels of stream nitrate in grab samples from over 200 unpolluted watershed forests in temperate South America and New Zealand (Perakis & Hedin 2002; McGroddy et al. 2008) are, on average, 10 times lower than the temperate data used here (which we restricted to sites with N losses measured over multiple years). Taking these data into account would change the tropical to temperate N loss ratio from near 10 to over 100, and change the proportion of this difference unexplained by climate alone from two- to fourfold to over 20- to 40-fold.

As is the case for all ecological studies, we did not take all possible drivers into account in our analysis. While restricting our comparison to forests receiving > 1500 mm per year rainfall greatly simplified our analysis of climate effects, we did not account for effects of high rainfall intensity or overland flow, which are thought to be important hydrological features of some tropical forests (Elsenbeer 2001) and which could, hypothetically, violate the assumption that plant uptake exceeds leaching losses (k_p >> k_l). However, increasing water throughput (i.e. increasing k_l) would dilute N concentration in leachate. Many temperate rainforests are also subject to high rainfall intensity (Vanderbilt et al. 2003; McGroddy et al. 2008). Furthermore, some of the most N-rich mature tropical forests show little variation in base flow stream nitrate concentrations between wet and dry seasons (Newbold et al. 1995). Similarly, while overland flow may serve as a short-cut to stream waters for nitrate in rainfall, it is by no means ubiquitous across tropical forests (Newbold et al. 1995; Elsenbeer 2001). We expect that incorporating such hydrological mechanisms would probably not affect our main results.

Another potentially important effect we did not take into account is temporal asynchrony in supply and demand, which can produce large pulses of N losses when N supply exceeds demand. However, our conclusions are based on multi-year watershed records from tropical forests that show consistently high DIN concentrations. These records show no evidence that the large interbiome difference in long-term means is attributable to such episodic losses. In addition, we suggest that tropical forests are unlikely to experience substantially greater N losses due to asynchrony than temperate forests (in fact, the opposite may be true due to the prolonged period of inactivity during temperate winters), and so including asynchrony in our model would probably not change our basic conclusions.

Our results highlight major uncertainties about the origin and dynamics of N inputs necessary at steady state to balance such high loss rates from mature tropical forests. Reported levels of N inputs from atmospheric deposition vary widely across the global tropics (e.g. Bruinzeel 1991). Global models suggest that pre-industrial atmospheric N deposition rates on terrestrial surfaces were probably only slightly higher in the tropics vs. temperate zones (Holland et al. 1999; Dentener et al. 2006), and levels required to balance current outputs are similar to those observed only in highly polluted temperate forests subject to long-term fossil fuel derived N inputs. While there is increasing evidence for accelerating N deposition inputs to remote tropical regions resulting from industry, agriculture and biomass burning (Chen et al. 2010), it remains unclear as to how to extend these findings both spatially and temporally, given that many of the most N-rich tropical forests are not thought to be exposed to chronic pollution. Our understanding of terrestrial N retention comes largely from observations of northern hemisphere temperate forests where elevated N inputs require decades of integration in the ecosystem before losses increase substantially. Given the observed loss rates from tropical forests summarised here, this further suggests that many tropical forests exist in a state of N saturation similar to some polluted northern hemisphere temperate forests (Aber et al. 1998).

Researchers have long hypothesised that symbiotic and/or asymbiotic BNF may contribute significantly to high N pools and accumulation rates in tropical soils (e.g. Jenny 1950; Jordan & Herrera 1981; Houlton et al. 2008). Recent studies indicate that symbiotic BNF in the tropics is highly facultative, tending to down regulate in N-rich closed canopy forests, but responding rapidly to disturbance and light availability (Hedin et al. 2009; Barron et al. 2011). Elsewhere, it has been shown that, if it is able to change rapidly, facultative BNF should only increase N stocks until the system reaches co-limitation with P or some other limiting resource, resulting in relatively low N losses (Hedin et al. 2009; Menge et al. 2009a). Large ecosystem N losses, however, are more consistent with an obligate symbiotic BNF strategy in which fixation rates are constant, regardless of supply in soils (Hedin et al. 2009), which appears unlikely in tropical forests, or a facultative strategy with time-lags between the ‘sensing’ of soil N availability and nodule construction (Menge et al. 2009a). The litterfall data we use to estimate mineralisation differences implicitly take symbiotic BNF into account, but cannot disentangle these symbiotic BNF dynamics.

Free-living BNF in surface soils or in the plant canopy can also fix substantial quantities of N in tropical forests (Barron et al. 2009; Cusack et al. 2009; Reed et al. 2011). In contrast to symbiotic BNF, asymbiotic BNF may be largely decoupled from plant N availability, and therefore represents a mechanism that can account for continued N inputs to an N-saturated ecosystem (Hedin et al. 2009). A recent review showed that rates of free-living BNF may be up to five times higher in tropical versus temperate forests (Reed et al. 2011). Our analysis takes this interbiome difference into account, and is consistent with the idea that asymbiotic BNF helps drive large N_l losses in tropical forests (part of the ‘leaky nitrrosat’ model of Hedin et al. 2009), as long as plants are not limited by N.

Resolving the sources and dynamics of N in tropical forests is critical to understanding how this vast biome interacts with and feeds back to the larger Earth system and how these forests will respond to increasing atmospheric pollution and disturbance. Our simple analysis has shown that, under the assumptions provided here, high N_l losses from many tropical forests probably result from a lack of N limitation at the ecosystem scale. These results imply that N availability across much of the tropics is unlikely to constrain the strength of the plant sink for anthropogenic carbon. As a result, increasing N deposition will probably result in even higher nitrate loading to many tropical surface waters and greater emissions of the heat-trapping gas nitrous oxide.

ACKNOWLEDGEMENTS

We are thankful to four anonymous referees for valuable comments on the manuscript. This work was supported in part by grants from the A.W. Mellon Foundation, the NSF (DEB-0614116), and NOAA to L.O.H.
Nitrogen saturation in tropical rainforests


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Litterfall N in mature humid forests worldwide from Vitousek (1984) and Vogt *et al.* (1986).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organised for online delivery, but are not copy edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Brenda Casper
Manuscript received 4 August 2011
First decision made 3 September 2011
Manuscript accepted 21 September 2011