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Elevated tropical nitrogen deposition interacts with global warming via changes in forest soil trace gas emissions

Most organisms cannot use nitrogen (N) directly from the large but inactive atmospheric N₂ pool. Therefore, N was one of the most important nutrients limiting crop production until the ‘Haber–Bosch process’ to ‘activate’ atmospheric N₂ and transfer it into bio–available N compounds was developed. Since the 1940s, this industrial N–fertiliser production has increased exponentially [1].

The Haber–Bosch process enabled humanity to meet the globally growing

demand for food and fibre. But, it also increased the amount of ‘reactive’ N (N_r) cycling through the environment, and greatly transformed the global N cycle.

Fossil fuel combustion, biomass burning and the cultivation of N–fixing plants like legumes also increased the formation of N_r compounds. In recent decades, anthropogenic N_r production has exceeded the natural terrestrial production from, for instance, N–fixing bacteria. Greatly elevated N input has had detrimental environmental

effects such as groundwater pollution, decreasing forest productivity and biodiversity, and soil acidification [2].

One further consequence has been an increase in the amount of N_r which is lofted to the atmosphere and can then settle back out to the landscape. In pristine regions, this ‘N deposition’ falls below 0.5 kg N ha^{–1} yr^{–1}. In contrast, N deposition currently exceeds 30 kg N ha^{–1} yr^{–1} over large areas where industry and/or agriculture are concentrated.

Enhanced N deposition rates were first detected in highly industrialised temperate regions. Subsequently, also economically emerging tropical regions like southern China fell under the same influence. Currently, tropical N deposition is further increasing [3]. How will this elevated N input influence the biogeochemistry of tropical forests?

One potential effect is on the production and emission of climate-relevant trace gases in and from soils: nitric oxide (NO) and nitrous oxide (N₂O) are by-products emitted during microbial conversion of N compounds in the soil (soil N cycling), mainly during nitrification (the oxidation of ammonia to nitrate) and denitrification (the reduction of nitrate to N₂). If the N-oxide (NO + N₂O) emissions are relatively small compared to the amount of N cycling, the soil N cycle is termed 'conservative' whereas if gaseous emissions are larger the N cycle is called 'leaky'. Carbon dioxide (CO₂), which is respired by microbes during decomposition of organic carbon and by roots, is also emitted from soils ('soil respiration').

N₂O and CO₂ are long-lived greenhouse gases, N₂O also contributes to the depletion of the stratospheric ozone layer, and NO is involved in smog formation. Tropical forest soils are the largest natural source of terrestrial N₂O, the third-largest natural source of NO, and cycle more than 10% of the atmospheric CO₂ through photosynthesis, respiration and microbial decay each year [4, 5, 6].

Elevated N deposition is expected to further increase soil N-oxide emissions, and may influence the soil respiration of tropical forests via changes in root and microbial activity. Such alterations in soil trace gas emissions would in turn affect atmospheric chemistry and Earth's climate.

Just a handful of studies have investigated how elevated N input affects tropical forest soil emissions of climate-relevant trace gases. Regarding N-oxides, the most comprehensive study has been conducted in Hawaii where short-term soil N-oxide emissions (which are occurring within one

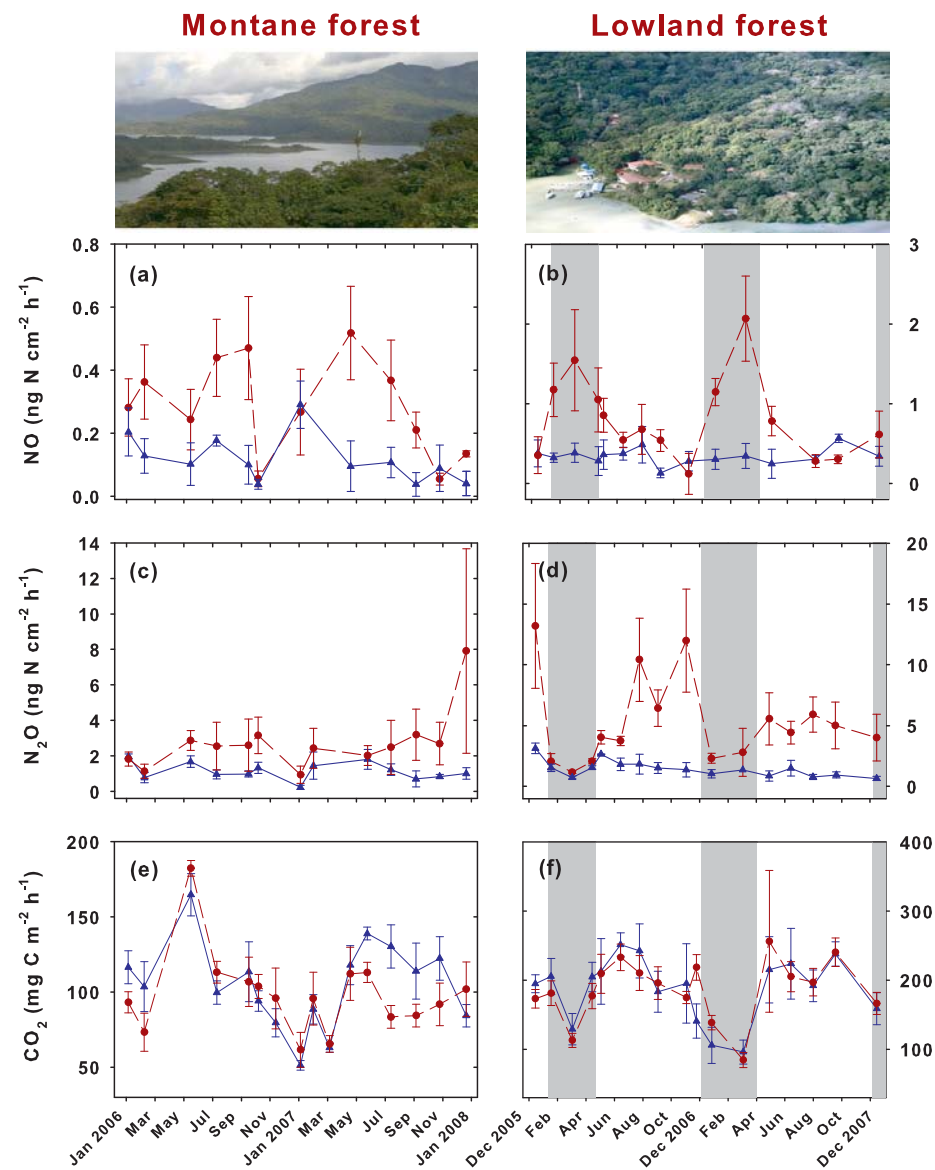


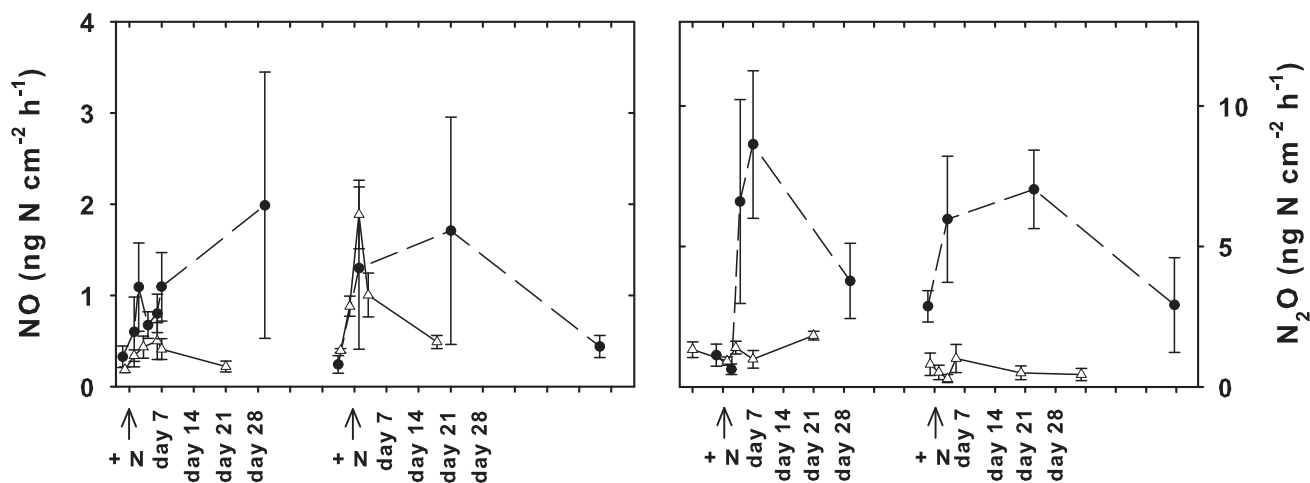
Figure 1. Mean (\pm standard error) chronic soil trace gas fluxes from the tropical montane (left panels) and lowland forest (right panels) with a), b) nitric oxide, c), d) nitrous oxide and e), f) carbon dioxide fluxes in the unfertilized control plots (\blacktriangle) and in the nitrogen-addition plots (\bullet). Grey shadings mark the dry seasons in the lowland forest. In the montane forest, first N addition was in February 2006; in the lowland forest, N addition started in 1998.

month following experimental N addition) were similarly large in 1–2 year and 5–6 year N-addition plots. Regarding CO₂, a study in Costa Rica found a boost of soil respiration [8] whereas a study in China reported a decline [9] under elevated N input.

To better understand the diverse results obtained in Costa Rica and China and on different soil types in Hawaii, we initiated N-addition experiments in two old-growth tropical forests in Panama: a N-limited montane forest with initially conservative soil N cycling, and a N-rich lowland forest where

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N cycling was leaky compared to the montane forest but conservative compared to many other N-rich lowland forests.

Litter decomposition was rapid in the lowland forest whereas the montane forest mineral soil was covered with several centimetres of organic material. N concentrations and cycling rates are usually larger on a mass basis in soil organic layers than in mineral soils of tropical forests [10]. This matters for soil N-oxide emissions. The mass of the organic layer is small, however, and its large N cycling rates may be unimportant on an areal base [10], for instance, for forest N nutrition and overall soil N-cycling characteristics.

Our experiments consisted of four control (un-manipulated) and four N-addition plots, 40 x 40 m in size, with the latter receiving 125 kg N ha⁻¹ yr⁻¹ split in four equal doses. Initially, soil N-oxide and CO₂ emissions were larger from the lowland than the montane control forest (Fig. 1). These control emissions were compared to those measured within the first two years of N addition in the montane forest, and after first-time as well as long-term (9–10 years) N addition in the lowland forest.

In the montane forest, soil N-oxide emissions increased immediately during the first week following first-time N addition (Fig. 2). In addition to measuring this immediate emission response (similar to the study in Hawaii), we determined ‘chronic’ fluxes, which we defined as those measured at least 6 weeks after an N addition when the immediate ‘fertilisation peaks’ had passed. In the 1–2 yr N-addition plots, the mean annual chronic emissions were twice as large as in the control plots (Figs. 1a and c).

Figure 2. Mean (\pm standard error) soil nitric oxide (left side) and nitrous oxide emissions (right side) from the first-time nitrogen-addition montane (●) and lowland (Δ) forest following two subsequent nitrogen additions marked with ‘+N’ below the x-axis.

In the lowland forest, first-time N additions caused only small and delayed increases in short-term soil N-oxide emissions (Fig. 2). In the 9–10-yr N-addition plots, mean annual chronic emissions were four times as large as in the control plots (Fig. 1b and d).

The opposing results of the Hawaiian N-addition study [7] and ours [11] show that N limitation of tree growth might not be a good predictor for the onset of elevated N-oxide emissions in general. Many tropical montane forests are N-limited and exhibit conservative soil N cycling, but an organic layer covers the mineral soil. If N-cycling rates in this organic layer are large and are immediately boosted by N addition, as observed in our study [11], soil N-oxide emissions will also increase without delay.

Regarding N addition to mineral soils without an organic layer, as usually the case

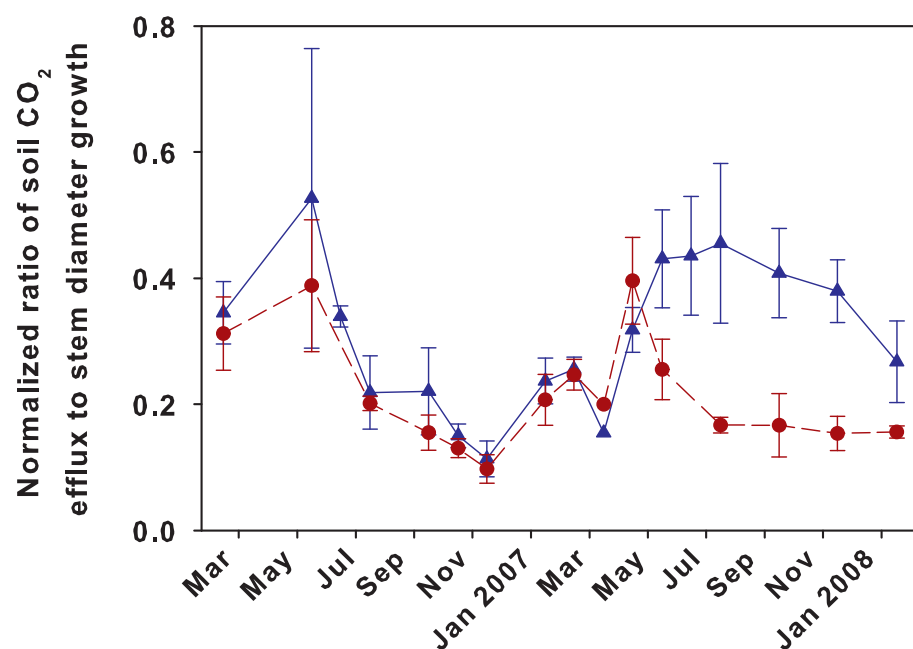


Figure 3. Mean (\pm standard error) normalised ratio of soil carbon dioxide efflux (‘soil respiration’) to monthly stem growth of trees with 0.3–0.5 m diameter at breast height from the control (▲) and nitrogen-addition (●) montane forest plots.

in N-rich lowland forests, the initial leakiness of the soil N cycle should be an important regulating factor in general. Thus, the leakier the N cycle the faster the N-oxide emissions will increase. The leakiness of soil N cycling varies in tropical lowland forests. It is, for instance, strongly affected by soil texture (e.g. sandy vs. loamy soil), which might therefore be a first proxy to qualitatively predict how quickly soil N-oxide emissions will increase.

Soil CO₂ emissions also changed in the montane forest, with decreases during the high stem-growth period (~ July to December) in the second year of N addition (Fig. 1e). This decline amounted to a 14% reduction of the annual soil CO₂ efflux compared to the control. The simultaneous promotion of stem diameter growth suggests that, as N limitation was alleviated, trees were able to invest more carbon to above-ground growth while less carbon was needed below ground for root growth and maintenance (Fig. 3).

In contrast in the lowland forest, soil respiration was unaffected by 9–10 years of N addition (Fig. 1f). This differs from the observed increase in soil respiration in Costa Rica [8]. A likely explanation for these contrasting results is that root responses on a smaller scale of nutrient manipulation (5 x 5 m study plots in Costa Rica) may differ from—and might not reflect—responses to fertilisation across entire root systems occupying larger soil volumes (40 x 40 m study plots in Panama).

With N addition ongoing, we expect that soil respiration will eventually decline, as reported from an N-saturated lowland forest in China [9]. Such a reduction can be caused by progressively adverse soil chemical characteristics which are induced by N enrichment. Indeed, soil pH and base saturation were smaller in the chronic N-addition than the control plots, while dissolved aluminium (Al) concentrations were larger. Above certain concentrations, Al is toxic for root and microbial activity. Our well-buffered lowland soil, however, still mitigated acidity- or Al-induced reductions of soil respiration after a decade of N addition [12].

In summary, elevated N deposition will cause substantial increases in soil N-oxide emissions from tropical forests, though the onset and magnitude of the effect will vary. The evidence for this response was consistent across different soil types in Hawaii [7], and was corroborated by our study in different Panamanian forest types. This increase in soil N-oxide emissions will contribute to global warming and affect atmospheric chemistry.

Effective policies and actions to decrease N mobilisation as, for instance, applying only the minimal amount of agricultural fertilisers necessary, could limit this consequence (please see the webpage of the 'International Nitrogen Initiative' for further information: www.initrogen.org).

Soil respiration from N-enriched tropical forests may eventually decline because of soil chemical changes, but this condition may take more than a decade to develop depending on initial soil characteristics and N-loading levels. However, if forest growth is N-limited, as is often the case in montane forests, soil respiration may also decline due to a shift in carbon allocation from below ground to above ground.

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