Impacts of biological nitrogen fixation on N₂O emissions from global natural terrestrial ecosystem soils: An Analysis with a process-based biogeochemistry model

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Abstract. Biological nitrogen fixation plays an important role in the global nitrogen cycle. However, the fixation rate has been usually measured or estimated at a particular observational site. To quantify the fixation amount at the global scale, a process-based model is needed. This study develops a biological nitrogen fixation model and couples it with an extant biogeochemistry model of N_2O emissions to examine the fixation rate and its effects on N_2O emissions. The revised N_2O emission model better matches the observed data in comparison with our previous model that has not considered the fixation effects. The new model estimates that tropical forests have the highest fixation rate among all ecosystem types, and decrease from the equator to the polar region. The estimated nitrogen fixation in global terrestrial ecosystems is 61.5 Tg N yr^{-1} with a range of 19.8 - 107.9 Tg N yr^{-1} in the 1990s. Our estimates are relatively low compared to some early estimates using empirical approaches, but comparable to more recent estimates that involve more detailed processes in their modeling. Furthermore, we estimate that the fixation contributes to -5% to 20% changes in N_2O emissions compared to our previous estimates, depending on ecosystem types and climatic conditions. This study highlights that there are relatively large effects of the biological nitrogen fixation on ecosystem nitrogen cycling and soil N_2O emissions and calls for more comprehensive understanding of biological nitrogen fixation and more observational data for different ecosystems to improve future quantification of the fixation and its impacts.

1. Introduction

In most terrestrial ecosystems, nitrogen (N) available for plants is generally limited although it is the most abundant element in the atmosphere (LeBauer and Tresder, 2008). It usually enters terrestrial ecosystems through processes of N deposition and from biological N fixation (BNF). Nitrogen deposition is a physical process, representing the direct input of reactive nitrogen (organic N, ammonia, and nitrogen oxides (NO_y) including nitric oxide (NO), nitrogen dioxide (NO_2), nitric acid (HNO_3) and organic nitrates) from the atmosphere to biosphere. BNF, a biochemical process that converts nonreactive nitrogen (N_2) to reactive nitrogen, provides a liaison between the atmosphere and biological systems. Lightning is also a way to convert N_2, adding 3-5 Tg N yr^{-1} to terrestrial ecosystems (Levy and Moxim, 1996). Nitrogen input via rock weathering is another important source for terrestrial ecosystems, adding 3-10 kg N ha^{-1} yr^{-1}(Morford et al., 2011; Houlton et al., 2018). BNF is significantly greater than lightening induced N fixation (Galloway et al., 1995). Taken together, natural N fixation is the primary source in the absence of human activities to global terrestrial ecosystems. For natural terrestrial ecosystems, the amount of N added is approximately balanced by the nitrogen converted back to the atmosphere (Stedman and Shetter, 1983) and lost into ocean and other aquatic systems.

Once entering terrestrial ecosystems, N can be taken up by plants and microbes, and converted into other oxidized forms through mineralization, nitrification and denitrification. In terrestrial ecosystems, N fixation generally affects the nitrogen cycle and nutrient level to constrain plant productivity. Any change of nitrogen input to terrestrial ecosystems will influence their soil N_2O emissions. Atmospheric N_2O absorbs infrared wave and reacts with ozone, affecting the global climate and atmospheric chemical conditions. On a per-unit-weight basis, N is almost 300 times more effective in trapping heat than carbon dioxide. Its atmospheric concentrations have increased from 286 ppb in 1950 to 327 ppb in 2015 observed in Cape Grim, Australia by the Advanced Global Atmospheric

Gases Experiment (AGAGE) Network, and in Alaska, Hawaii and South Pole by National Oceanic and Atmospheric Administration (NOAA). While the increase of concentration is significant due to rising industrial and agricultural emissions, natural ecosystems contribute about 60% of the increase (EPA, 2010). To date, the quantification of the trend and magnitude of N_2O emissions from natural terrestrial ecosystems is still with large uncertainties.

65 Furthermore, the effect of BNF in natural ecosystems on N_2O emissions has not been evaluated.

In the process of BNF, N_2 is converted to ammonia by certain soil microorganisms which can then be utilized by and incorporated into plants. In natural environment, N fixation is conducted by two types of microorganisms: asymbiotic organisms, including blue-green algae, lichens and free-living soil bacteria (Belnap, 2002; Granhall & Lid-Torsvik, 1975), and symbiotic organisms, such as fungi and nodule forming Rhizobium species. Among them,

70 the most dominant fixers are leguminous plants and their N fixation mechanisms are also best known (Sullivan et al., 2014; Vitousek et al., 2013). To date, the amount of N fixation by legumes is estimated in the range of 11.3-33.9 kg N ha^{-1} yr^{-1} (2.8~8.4 g m^{-2} yr^{-1}) in natural terrestrial ecosystems. A symbiotic relationship exists between legume plants and bacteria. In the process, legume plants provide the bacteria energy through photosynthesis, meanwhile, the bacteria around the rhizobia supply the legume N in the form of ammonia.

75 This study first models the BNF from the symbiotic relationship between legume plants and bacteria. The model is then coupled with an existing N_2O biogeochemistry to quantify the BNF impact on N_2O emissions from global terrestrial ecosystem soils.

2. Methods

2.1 Overview

80 We first develop a BNF model and then couple the model with an earlier version of N_2O biogeochemistry model (Yu and Zhuang, 2019). The revised model is then used to quantify the BNF at the global scale and its impacts on soil N_2O emissions from natural terrestrial ecosystems. The BNF rate estimates consider the effects of environmental conditions including temperature, soil moisture, soil mineral nitrogen content and soil carbon content. The new model is calibrated and evaluated with observed N fixation rate data from published studies for various

85 natural terrestrial ecosystems from the Arctic to tropical ecosystems. The model sensitivity to model input is analyzed. The model is then extrapolated to the global terrestrial ecosystems at a monthly step and a spatial resolution of 0.5° by 0.5° for the final decade of the 20th century. The effects of BNF and atmospheric nitrogen depositions on N_2O emissions from natural terrestrial ecosystem soils are analyzed.

2.2 Model Description

90 The Terrestrial Ecosystem Model (TEM) is a process-based model that simulates carbon and nitrogen dynamics, hydrological and thermal processes for terrestrial ecosystems. Although many efforts were made to incorporate more details of the N cycle, the N input from the atmosphere to ecosystems has not fully been incorporated to date, especially the BNF as input. Here we improve the N dynamics within TEM by considering N

95   fixation by legumes. The other calculations of carbon and N fluxes and pools are inherited from an earlier version of TEM (Zhuang et al., 2003; Yu and Zhuang, 2019).

BNF is the most significant process in either symbiotic or non-symbiotic forms converting stable molecular N_2 into N chemical compounds that are available to plants. For most terrestrial ecosystems, N fixer could be in many forms, such as free-living bacteria, lichens, and blue algae. But among them, symbiotic BNF is a dominant process to provide biologically accessible N, and most systematical BNF is regulated by legume plants, especially in

100 cropland and semi-natural environment (Mus et al., 2016). In natural environment, contribution from legume can be significant but with large uncertainties, which is greatly determined by various environmental conditions (Lindemann and Glover, 1996). In this study, the N fixation via legume plants is modeled considering (1) the accessible N concentration in soils, (2) the limitation of temperature, (3) soil water status, (4) the carbon demand for N fixation, and for spatial simulation, (5) the percentage of N fixing plants for each ecosystem type as:

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$$N_{fix} = N_{fixpot} f_t f_W f_N f_c f_{plant} \tag{1}$$

where N_{fixpot} is the potential N fixation rate (g N day^{-1}) , f_t is the influence function of soil temperature, f_W is the soil water function, f_N is the function of root substrate N concentration, f_C is the function of plant carbon availability, and f_{plant} is the function of legume plant coverage.

The potential N fixation is highly related to the total N demand of plants and the available nitrogen in soils.

110 Theoretically, the definition of potential N fixation rate should be the difference between the demand and supply of N. Both of them vary with plant types, stages of growth and soil conditions. For large spatial-scale simulations for various ecosystem types, it is impossible to derive potential N fixation because of data availability. N_{fixpot} can be estimated based on dry matter of root, nodule or plant dry matter (Voisin et al, 2003, 2007). However, root biomass is also difficult to measure directly. In most published studies, the potential nitrogen fixation rate was measured

115 using an acetylene reduction array (ARA) method (Hardy et al, 1968, 1973), and some used ^{15}N methods (Shearer and Kohl, 1986). In our simulation, N_{fixpot} is assumed to be a constant for each ecosystem type. The N_{fixpot} range is determined from literature and specific values for various ecosystem types are obtained through model parameterization.

Soil temperature is a controlling factor for both microbial activities and plant growth. A large number of

120 studies show that different plants have slightly different preferences for temperature (Montanez et al, 1995; Breitbarth et al., 2007; Gundale et al., 2012). For soybean, 20-35 °C is optimal (Boote et al., 2008), and for white clover the optimal temperature can be 13-26 °C (Wu and McGechan, 1999). The activity of microbes responds slightly differently to temperature among species. For most of them, the optimum temperature is 20-25 °C, and at 12-35 °C the activity is not limited. Generally, BNF increases as the temperature rises from minimum temperature

125 (0-5 °C) for N fixation to optimal temperature, maximum rate occurs within an optimal range (15-25°C), and decreases from optimal to maximum temperature above which BNF will stop at 35-40 °C:

$$f_t = \begin{cases} 0 & when \ (t < t_{min} \ or \ t > t_{max}) \\ \frac{t - t_{min}}{t_{optL} - t_{min}} & when \ (t_{min} \leq t < t_{optL}) \\ 1 & when \ (t_{optL} \leq t \leq t_{optH}) \\ \frac{t_{max} - t}{t_{max} - t_{optH}} & when \ (t_{optH} < t \leq t_{max}) \end{cases} \qquad (2)$$

where the upper limit (t_{max}) is set to 45 °C. There is no lower limit, but when t is low enough, f_t will be close to zero
130 (Wu and McGechan, 1999; Boote et al., 2008; Holzworth et al., 2014) (Table 1). For the convenience in computing,
a lower limit is set in our model. When the temperature goes beyond its upper or lower limit, f_t is assumed to be 0.

Water stress has a direct effect on nitrogen fixing system (Sprent, 1972). With proper temperature, soil
moisture condition is the major factor controlling nitrogen fixation rate (Srivastava and Ambasht, 1994). Soil water
deficit and flood dramatically inhibits N fixation because of drought stress and oxygen deficit, respectively (Omari
135 et al., 2004; Mario et al., 2007). In our model, the water factor is linearly related with soil water content (Williams,
1990; Wu and McGachan, 1999):

$$f_w = \begin{cases} 0 \ when \ (W_f \leq W_a) \\ \varphi_1 + \varphi_2 \ when \ (W_a < W_f < W_b) \\ 1 \ when \ (W_f \geq W_b) \end{cases} \qquad (3)$$

where W_f (J kg^{-1}) is the available soil water, which is defined as the ratio of water content to that at the field
capacity. In soils, water potential generally includes osmotic and matrix potentials, ranging from -0.1 to -0.3 bar for
140 typical soils, which has little effects on the N fixation. But when the soil gets very dry, the potential can be up to -
100 to -200 bar and increases rapidly. W_a is the bottom threshold below which N fixation is totally restricted by soil
moisture. W_b is the upper threshold above which nitrogen fixation is not limited by soil moisture. φ_1 and φ_2 are
parameters representing the linear relationship between soil water content and its effect on N fixation (Table 1).

It is generally thought that more substrate N in soils will slow down the N fixation, because plants can
145 uptake N directly from soil with less energy (Vitousek and Field, 1999). By comparison, N fixation needs more
energy and consumes more carbon than plant N uptake does. Thus, the N fixation is only considered to occur when
the direct N uptake from soil cannot meet the plant N demand. In our model, the inhibition effect of N is defined as
(Wu and McGehan, 1999):

$$f_N = \begin{cases} 1 - f_{Nup} ln(1000 - N_s) & when \ (N_s \geq 0.001) \\ 1 & when \ (N_s < 0.001) \end{cases} \qquad (4)$$

Where f_{Nup} is a parameter related to legume biological N fixation and soil N. N_S is the soil mineral N (g N m^{-2}).
BNF efficiency shows a natural logarithmic relation with the soil mineral N.

155 N fixers get photosynthetic carbohydrate support from plants. Because the product of every unit of nitrogen
consumes a certain amount of carbon, the lack of carbon supply will inhibit the N fixation. The carbon cost for per

unit of fixed N varies widely depending on environmental conditions and ecosystem types. For example, the consumption of carbon is only 1.54 times of fixed N for cowpea (Layzell et al., 1979), and it can be 6.3 to 6.8 times for soybeans (Ryle et al., 1979). It is also related to the life cycle of plants. The carbon effect is modeled following a

160   Michaelis-Menten equation (Boote et al., 1998):

$$f_C = \frac{1}{1 + K_c / C_r} \tag{5}$$

where C_r is the soil carbon content (g C m^{-2}) to represent carbon availability from plants to N fixers. K_c is the Michaelis-Menten constant, which is plant species dependent.

2.3 Data

165   The classification of land cover and leguminous biomes were derived from the combination of the International Geosphere and Biosphere (IGP) land-cover classification system and the study of Schrire et al (2005). The experimental N$_2$ fixation data for model calibration were collected for 7 major ecosystem types (Figure 1). Nitrogen fixation rates were determined with acetylene reduction assay (ARA) method in most published studies (Table 2, data were from Cleveland et al. (1999)), expressed in kg N m^{-2} yr^{-1}. Some of them were measured with the ^{15}N

170   natural abundance technique. Measurements of N$_2$O emissions affected by legumes were collected at 8 sites, including tropical rainforest in Brazil and Peru, tropical dry forests in Puerto Rico, temperate forest in New York, grassland in Germany and Scotland, and pastures in Australia and Costa Rica (Table 3). Monthly N$_2$O emission data were organized for comparison with model simulations.

The parameters for N$_2$ fixation module were initialized with *a prior* values (Table 2). Ecosystem-specific and

175   microbe guild-specific parameters were inherited from previous TEM model (Zhuang et al., 2003; Yu and Zhuang, 2019). The global simulations were conducted at a spatial resolution of 0.5 by 0.5 degree and at a monthly time step. Historical climate data including temperature, precipitation, cloudiness and water vapor pressure were derived from the Climate Research Unit (CRU) (Mitchell and Jones, 2005). Soil texture data were from Melillo et al. (1993) and Zhuang et al. (2003). Other initial conditions including vegetation properties, soil carbon content and soil nitrogen

180   contents were from Chen and Zhuang (2013) and Zhuang et al. (2012).

For regional simulations, the total amount of fixed N is also influenced by legume coverage. For each ecosystem type, we estimated the coverage according to the distribution of legume plants and field studies (Table 4, the coverage data are compiled from Cleveland et al., (1999)), where the minimum and maximum values were derived from the abundance of N-fixers.

185   ### 2.4 Model calibration and site-level validation

Most model parameters are legume-specific or vegetation-specific and are adjusted based on value ranges from previous studies (Table 1). Model is parameterized for 11 representative natural terrestrial ecosystems (Table 2). Root mean square error (RMSE) and coefficient of determination ($0 \leq R^2 \leq 1$) were used for model calibration. RMSE

190   was calculated to show the mean difference between simulated data and observational values. The model is iterated
with changing parameters until the RMSE reached a certain value for each site. Most parameters in the model
driving nitrification and denitrification have been defined and calibrated in previous studies (Yu and Zhuang, 2019).
The calibrated model is evaluated at the site level (Table 3) and then extrapolated to the global terrestrial
ecosystems.

        To evaluate the model's performance on capturing seasonal trends, the simulated N_2O emissions were plotted
195   along with observational data for the observational period. A linear regression is conducted to show the similarity
and discrepancy between simulations and observations, R^2, along with the slope and intercept of the linear
regression line are calculated. Six field observational sites having legume were organized for the model validation
(Table 3). Monthly N_2O emission data were used for model comparison.

2.5 Model Sensitivity and Uncertainty Analysis

200   The response of N fixation and N_2O emissions of different biomes to input data, and parameters was analyzed
using sensitivity test. Four major input variables were selected, including air temperature, precipitation, soil nitrogen
content and soil organic carbon content. The monthly average input variables were changed by ±10% of the original
level for each site and each grid. The variables were changed at 6 levels, respectively, and the rest of input variables
were kept at their original values. The sensitivity was calculated by comparing the simulated annual N_2O emissions
205   and nitrogen fixation to the simulations with the original input values (Figure 2).

3. Results

3.1 Model evaluation

        To evaluate the model, thirty-five observational sites were selected for 7 major ecosystem types across the
globe, representing different climate and soil conditions. The experimental data of N fixation have a mean value of
210   12.9 kg N ha^{-1} yr^{-1}, with a standard deviation of 17.7 kg N ha^{-1} yr^{-1}. The maximum observed fixation occurred in
temperate forest in New Zealand, while the minimum rate was also for temperate forest in Idaho State of the US.
Our simulations are comparable with the observed data for all major ecosystem types with the coefficient of
determination (R^2) of 0.44 and with a slope of 0.46 (Figure 3). The regression results are mainly influenced by some
observed data greater than 30 kg N ha^{-1} yr^{-1} (mean + standard deviation). By removing these data, the slope of
215   regression increases to 0.72. Observational data for temperate forests show the greatest variation among all major
ecosystem types, with a maximum value reaching 800 times of the minimum one. Simulations are closer to the
observations across sites in temperate forests with R^2 of 0.26 and slope of 0.42. Our model underestimated nitrogen
fixation rate in temperate forests. The large variation in observations may be due to the distribution of legume
plants, different sampling time periods (e.g., growing and non-growing seasons), and varying climate conditions.
220   For tropical forests, our model estimates of N fixation are higher than observations with the slope of 0.75 and R^2 of
0.44.

The model was also tested by comparing the simulated N_2O emissions with observed data for 5 sites and 3 ecosystem types including tropical forests, temperate forests, and grasslands. All observed data were converted into monthly average values. Our model reasonably reproduced the seasonal variations of N_2O emissions at

225   observational sites. In our earlier version of the model, the biological nitrogen input was assumed to be a constant throughout the year (Yu and Zhuang 2019). Compared to our earlier version, the current version contributes 5% to 20% of the total N_2O emission, but only leads to a minor difference to total seasonal trend throughout the year (Figure 3). There are still some discrepancies between simulated and observed N_2O emissions, which could be due to the uncertainty in measurement, sudden weather events and changes in soil characteristics. The comparison

230   between measured and simulated data further shows the influence of BNF for different ecosystem types on N_2O emissions. The influence is larger in tropical areas, while by percentage, BNF is more important for grasslands in temperate regions.

3.2 Model sensitivity analysis

The model sensitivity analysis quantifies the impact of changes in forcing data on nitrogen fixation rate and

235   N_2O emissions. Climate conditions including air temperature and precipitation, and soil characteristics of nitrogen content and carbon content varied at 3 levels to examine the sensitivity. The response of nitrogen fixation rate and N_2O emissions is quantified for each ecosystem type. The sensitivity test was conducted for all observational sites (Table 2 and Table 3). Temperature is the most sensitive variable (Figure 2). Comparing to N_2O emissions, nitrogen fixation is more sensitive to the change of all forcing conditions. Increasing soil nitrogen results in a lower N

240   fixation, but increasing N_2O emissions. Abundant soil nitrogen content inhibits BNF activity, but stimulates nitrification and denitrification processes.

3.3 Biological nitrogen fixation in global terrestrial ecosystems

Tropical forests in South America, Central Africa and South Asia show a wide range of N fixation rate between 1 and 200 kg N ha^{-1} yr^{-1} (Bruijnzeel et al, 1991). Here all plants in tropical rainforest are assumed to fix nitrogen and

245   one set of parameters are applied for all tropical forests. The coverage for tropical forests in the landscape was assumed to be 15% (Cleveland et al., 1999), ranging from 5% to 25%. The N_2 fixation rate was estimated to be 18.2 kg N ha^{-1} yr^{-1}, which is the highest among all vegetation types. Our simulations show that the total fixed nitrogen ranges from 10.8 Tg N yr^{-1} to 54 Tg N yr^{-1}, with the average value of 32.5 Tg N yr^{-1}(Table 4). Nitrogen fixation in tropical forests is almost half of the global total amount and a principal contributor of BNF in natural ecosystems.

250   Tropical forests have the largest potential to fix nitrogen given that the optimal temperature and soil moisture for BNF is relatively easy to have under tropical climatic conditions.

Temperate forests cover the largest land area from 30°N to 60°N, including temperate coniferous forest, temperate deciduous forest and temperate evergreen forest. Temperate areas have the majority of legumes and many temperate ecosystems are considered to be N limited. Comparing to other ecosystem types in temperate regions,

255   conifers are likely to limit the reproduction of legumes (Wheatley et al, 2010). In general, plant species carrying nitrogen fixers are only distributed in a small percentage of natural temperate forests, like clear-felled areas and pastures (Boring and Swank, 1984). Cleveland et al. (1999) indicated that the legume coverage ranges from 1% to 10% of the land area only. Consequently, our simulations indicate that N fixation by temperate forests was 12.7 kg N ha^{-1} yr^{-1}. The estimates of the total nitrogen fixation were between 1.9 and 19.14 Tg N yr^{-1} (Table 4). Nitrogen

260   fixation in temperate areas contributes 12.5% of the global total amount.

Savanna covers over a half of African continent, Australia and large areas of South America. It is an important biome in the Southern Hemisphere. There is a great variation in native legume species. Only in humid savanna, legumes may significantly contribute to the increase of soil nitrogen (Cech et al., 2008). On average, 15% of the vegetation in savanna is considered as legume grass and biological nitrogen fixation occurs when precipitation is

265   greater than 10 mm per month. Generally, nitrogen fixation in savanna is restricted by soil moisture, while temperate grassland is limited by both temperature and soil moisture (Bustamante et al, 1970). Nitrogen fixers are not abundant for these biomes (Woodmansee et al., 1981). The coverage of nitrogen fixers was assumed to be from 5% to 25%, (Cleveland et al., 1999). Our simulation assumed that nitrogen fixers cover 15% of the land, resulting in 1.9 kg N ha^{-1} yr^{-1} fixation, representing a much smaller fraction compared to forest ecosystems. Total fixed nitrogen in

270   grasslands appeared to range from 0.62 to 3.1 Tg N yr^{-1}, with an average of 1.86 Tg N yr^{-1}. For savanna, the total contribution was less due to its relatively small area. The minimum, average and maximum values were estimated to be 0.45, 1.34 and 2.23 Tg N yr^{-1}, respectively.

In tundra and boreal forest regions, both host plants and their rhizobia are adapted to the environment with low temperature. Nitrogen fixation rate is extremely variable for boreal ecosystems. For tundra, the coverage was

275   assumed to be 3-15%, and for boreal forest, the coverage was 4-18%. But in general, the low temperature and permafrost conditions limit the activity of nitrogen fixers (Alexander, 1981). We estimated that tundra ecosystems fix nitrogen at 3.2 kg N ha^{-1} yr^{-1}. Their total BNF was between 0.51 to 2.55 Tg N yr^{-1} with average of 1.54 Tg N yr^{-1}. In boreal forests, the fixation rate was much lower (2.1 kg N ha^{-1} yr^{-1}) compared to temperate forests.

In deserts, although some legumes may exist in extremely dry conditions, and some species may grow rapidly

280   after rainfall, their fixation could be neglected. However, in semi-arid areas, legumes are common plants with several species, their N fixation is lower than tropical and temperate forests (5.7 kg N ha^{-1} yr^{-1}).

Mediterranean ecosystems such as in south California and some areas in South Australia are characterized with mild rainy winter and hot dry summer, containing both evergreen and deciduous shrublands, in which nodulated legumes are prominent (Sprent et al., 2017). These legumes are more active in comparatively wet season than in dry

285   season (Sánchez-Diaz, 2001). The ability to fix nitrogen is considered to be one of the most important features that enable legumes and plants to survive under severe environments (Crisp et al., 2004). We estimated that the N fixation rate of these legume species is similar to that in grasslands (2.7 kg N ha^{-1} yr^{-1}).

Spatially, the highest rate of N fixation occurred in the tropical and sub-tropical areas, as a result of proper climate and soil characteristics for fixers (Figure 4a). N fixation from tropical forests and xeric shrubland contributes

290   to nearly half of the global terrestrial amount (Table 4). A lower N fixation rate was in high latitudes of East China, North America and Europe, which were mainly covered with temperate forests. Compared to tropical areas, N

fixation in temperate regions shows a larger variability depending on vegetation types. The spatial variation could be attributed to the distribution of legume plants, in addition to the difference of humidity and temperature conditions. N fixation in temperate regions accounts for 35% of the total fixed N.

295 **3.4. Soil N₂O emissions enhanced by biological nitrogen fixation**

The model was run at site level to estimate the role of BNF on N₂O emissions. Our analysis between current model and previous model without N fixation module indicated that N₂O emissions would be affected by -5% to 20% depending on biome types and seasons (Figure 5). The involvement of BNF strengthens the seasonal variation as BNF led to lower emissions in winter and higher emissions in summer. Our model estimated that high BNF rates

300 in growing season is consistent with other regional and global estimates (Cleveland et al., 1999, 2013; Lee and Son, 2005; Lett and Michelsen, 2014). The energetic cost for active N uptake becomes lowest when soil temperature is around 25°C (Fisher et al. 2010). Similarly, our estimates of high BNF rates also occur at similar temperature conditions in spring and summer. The global soil nitrogen mineralization rate was estimated to be 696 Tg N yr⁻¹ while 15% of plant N demand was provided by BNF (Cleveland et al., 2013). Our estimates of BNF were lower

305 than the estimates by Cleveland et al. (2013) and fell within 10% of the total soil mineralization rate. This result also indicates that about 10% of the mineralized N was induced by BNF. As mineralized nitrogen is the substrate for subsequent reactions producing N₂O, the additional N input through BNF to terrestrial ecosystems led to the change of N₂O emissions across biomes.

During 1990-2000, our simulations show that BNF in natural terrestrial ecosystems is 61.5 Tg N yr⁻¹, but

310 anthropogenic N fixation was much higher at 140 Tg N yr⁻¹ (Galloway et al., 2002). This large amount of anthropogenic N input to terrestrial ecosystems is expected to inhibit the natural BNF and might lead to less BNF in the future. Our simulations indicate that BNF has a minor influence on N₂O emissions for most high latitude ecosystems and extremely arid regions, as a result of low temperatures and drought (Figure 4b). Overall, the fixation as additional N to soils led to -5% to 20% changes in soil N₂O emissions.

315 **4. Discussion**

4.1 Comparison with other estimates of biological nitrogen fixation

There is a large uncertainty in estimating the N input into terrestrial ecosystems, especially from BNF (Sutton et al., 2014) (Table 4). In our study, a calibrated process-based model was applied to estimate site-level and global BNF in natural terrestrial ecosystems. Empirical models provide reasonable estimation based on relationships between fixation rate and environmental factors (e.g. evapotranspiration) (Cleveland et al, 1999), while process-

320 based approaches consider processes in BNF affected by multiple controlling factors (Fisher et al., 2010; Gerber et al., 2008; Meyerholt et al., 2016). Our estimated BNF in the global terrestrial ecosystems is 61.5 Tg N yr⁻¹ with an uncertainty ranging from 19.8 to 107.9 Tg N yr⁻¹, which is lower than most existing studies. Cleveland et al. (1999) provided a central value of 195 Tg N yr⁻¹ by scaling up field-based experimental data, with a range of 100 - 289 Tg

325 N yr^{-1}. This range represents potential distribution of nitrogen fixation. In reality, N fixation is also affected by climate and soil conditions, making the actual terrestrial BNF smaller than the potential one. In a more recent study of Cleveland et al. (2013), a total of 127.5 Tg N yr^{-1} was estimated to be related to BNF, based on the relationship between BNF and evapotranspiration (ET). Galloway et al (2002b) also provided several estimates for global BNF. Galloway et al. (2004) further suggested a range of 100 - 290 Tg N yr^{-1} and implied that the true rate of BNF would

330 be at the low end of this range without large-scale human disturbance. In an earlier study (Galloway et al., 2002b), the mean annual global BNF was estimated to be 89-100 Tg N yr^{-1}. By assuming a steady state between N input to and loss from ecosystems, Vitousek et al. (2013) estimated the BNF to be 58 Tg N yr^{-1} with a plausible range of 40 - 100 Tg N yr^{-1}, which is similar to our estimates. However, Xu-Ri and Prentice (2017) estimated that the N fixation was about 340 Tg N yr^{-1} which is almost 5 times larger than our estimates. In their study, BNF was determined by

335 plant N requirement across all biome types.

In our estimation, tropical forests significantly contribute to the total BNF, which is up to 18 kg N ha^{-1}yr^{-1}. This result is highly related to the density of leguminous plants, and the physical conditions in tropical areas (Crews, 1999). Our simulated results are comparable to the estimates of symbiotic N$_2$ fixation from tropical evergreen (5.5-16 kg N ha^{-1} yr^{-1}) and deciduous forests (7.5-30 kg N ha^{-1} yr^{-1}) (Reed et al., 2011). Barron et al. (2010) directly

340 measured N$_2$-fixing root nodules across lowland tropical forests and their observations also showed a large variation among individual trees. For a mature forest matrix, the average value was around 10 kg N ha^{-1} yr^{-1}, but it could be as high as 200 kg N ha^{-1} yr^{-1} for some areas. Cleveland (2013) provided a similar estimate to ours (around 12 kg N ha^{-1} yr^{-1}), but higher values (20-30 kg N ha^{-1} yr^{-1}) in their earlier studies (Cleveland et al., 1999). Sullivan et al (2014) analyzed human's impact on tropical N fixation and found, depending on forest ages, fixation was 5.7 kg N ha^{-1} yr^{-1}

345 with a range from 1.2 to 14.4 kg N ha^{-1} yr^{-1}, which is lower than our estimates.

For temperate and boreal forests, we estimated that BNF fixation is 2.1-18 kg N ha^{-1} yr^{-1}. The existing BNF estimates from literature also show a large uncertainty for those forest ecosystems. For instance, LM3V-N model (Gerber et al., 2009) suggested that the N input to forests to be less than 5 kg N ha^{-1} yr^{-1}. But their model also estimated that, in moist forests, the uptake of N could be 30-80 kg N ha^{-1} yr^{-1}. Deluca et al. (2002) reported that

350 cyanobacterium and feather moss could act as a supplement to N fixation in boreal forests (0.5 kg N ha^{-1} yr^{-1}) while the organic N accumulation could be 3 kg N ha^{-1} yr^{-1}. For the forests in northwest Rocky Mountain, N fixation amount is on average between 0.5 and 2 kg N ha^{-1} yr^{-1} (Clayton and Kennedy, 1985; Fahey et al., 1988) while Kou-Giesbrecht and Menge's model (2019) estimated the N fixation rate to be 0 -10 kg N ha^{-1} yr^{-1} for temperate forests, and 0 to 6 kg N ha^{-1} yr^{-1} for boreal forests.

355 There could be a number of reasons for our comparatively lower estimates. The most important one is that there is a considerable uncertainty in estimating the coverage of N fixing plants. High diversity in the distribution of legume plants highly influences the estimation of total plant coverage, because our estimation was based on site-level experimental data. In order to improve our understanding, more investigation on legume plant distribution and associated data for N fixers is needed, especially in the Middle Asia, South America and Africa.

360 Large variations of BNF rates exist across terrestrial ecosystems spatially (Figure 4a). The global BNF spatial pattern is similar to other estimates (Cleveland et al., 1999; Xu-Ri and Prentice, 2017). The highest N fixation rate in

tropical regions (more than 50% of the global terrestrial N fixation) is primarily due to their warm and moist soil
conditions. Further, N fixed by human activities became increasingly influential in the past century (Galloway et al.,
2002), especially in temperate regions due to their large human population. The anthropogenic N deposition
365   contributed more to soil N than BNF did. As a result, soils became N rich, inhibiting BNF in temperate soils. This
could explain why the potential N fixation rate was high in temperate ecosystems, but only contributed to 20% of
the total fixation.

4.2 Major controls to biological nitrogen fixation

In our simulations, the N fixation was primarily influenced by soil temperature, moisture and soil nitrogen
370   content. The highest N fixation rate in tropical ecosystems is consistent with our sensitivity analysis for temperature
and soil moisture. The sensitivity analysis indicated that a 1-3°C increase of temperature led to 7% increase in N
fixation rate. Nitrogen cycle responds differently between different biomes and legume types. But in general,
increasing temperature will accelerate processes in the N cycle. Soil moisture correlates with BNF in a similar way
with temperature. A slightly increase of precipitation (10%) increased the nitrogenase activity. However, the
375   response of N fixation to soil water stress is not as sensitive as that to the change in temperature. Xeric shrubland
and savanna in dry tropical areas still contribute greatly to the global N fixation, while the contribution of boreal
forests, with abundant rainforest and low temperature, is much lower.

BNF is highly regulated by soil nitrogen content. N-deficiency conditions usually favor BNF activities, for
example, in xeric shrubland and savanna. Enhancing soil N content will decrease the N fixation rate, which is also
380   consistent with our sensitivity analysis. It costs less energy for plants to take up N directly from soils rather than
biologically fixing it from the atmosphere (Cannell and Thornley, 2000). However, there is an exception for some
areas in tropical ecosystems. Many tropical soils are comparatively rich in nitrogen, but N-fixing plants are still
active to compensate the nitrogen depletion due to the rapid N cycling (Pons et al., 2007). This explains why N
fertilization inhibits the BNF in temperate ecosystems, but BNF is still active in N-rich soils in tropical ecosystems.
385   In areas where the energetic cost succeeds the demand of N, the BNF rate will be comparatively lower. Sullivan et
al. (2014) suggested that there were lower rates of BNF in undisturbed mature forests and higher rate in secondary
forests, depending on the balance between N-demand and energy consumption.

4.3 Model limitation and future work

The incorporation of BNF into TEM allows us to more adequately estimate N_2O emissions from natural
390   terrestrial ecosystems. However, there are several limitations in this study.

First, the current model ignores the effect of free-living BNF. Although symbiotic BNF is critical for most
natural and semi-natural ecosystems, asymbiotic organisms play an important role in extreme environments such as
waterlogged soils and deserts. The importance of symbiotic BNF or fixation by leguminous plants may not be as
significant as previously thought. Elbert et al. (2012) suggested that cryptogam contributed nearly half BNF in

395 terrestrial ecosystems, which was up to 49 Tg N yr^{-1}. In some tropical areas, the spatial N input from free-living
bacteria even exceeds symbiotic input (Sullivan et al., 2014). In addition, legumes are not the only source of
symbiotic BNF. Some fungi species have the ability to actively fix atmospheric nitrogen. But in most existing
models, fungi or mycorrhizae symbioses are not considered due to the limited knowledge about their mechanisms of
fixing N (Fisher et al., 2010). A more comprehensive model that covers various types of nitrogen fixation is needed.

400 Second, the BNF process in our model is calibrated with a limited amount of data, imposing a general set of
parameters to all plant species and soil conditions within an ecosystem type. More observational data from natural
terrestrial ecosystems is desirable to improve our model.

Third, it is difficult to isolate the N addition via natural processes from human activities. In the US, 20-35% of
annual N input into terrestrial ecosystems are human-related (Sobata et al., 2013). As a result, the quality of

405 observational data varies from site to site, some BNF data are only semi-natural. The observational data are
imperfect, which might have also biased our estimates through model parameterization process.

5. Conclusions

This study developed a process-based biological nitrogen fixation model and coupled it with an extant nitrous
oxide emission model. The model was evaluated with observed data for both N fixation and N$_2$O emissions. The

410 model was then extrapolated to the global natural terrestrial ecosystems. Our model estimated that biological
nitrogen fixation in natural terrestrial ecosystems was 61.5 Tg N yr^{-1} during the last decade of the 20th century and
the greatest fixation rate occurred in tropical regions. Soil temperature, rather than soil moisture and nutrient
content, is the most dominant control to the fixation. We further found that, the fixation as additional N to soils led
to -5% to 20% changes in soil N$_2$O emissions. Both the new and previous models were able to capture the seasonal

415 variation of field-observed N$_2$O, but the new version of the model estimated more seasonal dynamics. Lacking the
knowledge about the distribution of N fixing plants and their physiological features might have biased our estimates
of both biological nitrogen fixation and N$_2$O emissions at the global scale.

Data availability

420 Climate data including monthly cloudiness, precipitation, temperature, and water vapor pressure are from the
Climate Research Unit (CRU) http://www.cru.uea.ac.uk/data (last access: May 2017). Global vegetation data and
soil data are available in Zhuang et al. (2003) and McGuire et al. (2001). The explicit spatial data on soil water pH
from the ORDL gridded soil properties product (https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=546, last access:
March ,2017) are based on the World Inventory of Soil Emission Potentials (WISE) database (Batjes, 2000). The

425 global average carbon dioxide concentration is observed at NOAA's Mauna Loa Observatory. N deposit data are
from NADP monitor and CASTNET. The initial values of soil microbial carbon and nitrogen, and the ratio of C/ V /
N at the global scale, were from a compilation of global soil microbial biomass carbon, nitrogen, and phosphorus
data (https://doi.org/10.3334/ORNLDAAC/1264, last access: May, 2017). *The data presented in this paper can be
accessed through our research website (http://www.eaps.purdue.edu/ebdl/).*

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Author contribution

Q. Zhuang and T. Yu designed the research. T. Yu performed model simulations and data analysis. Both authors contributed to the paper writing.

435 **Competing interests**

The authors declare that they have no conflict of interest.

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Table 1. Description of parameters used in the model

Parameters	Description	Unit	Reference Value	reference
N_fix	nitrogen fixation rate	g N m^{-2} day^{-1}		
N_fixpot	potential nitrogen fixation rate	g N m^{-2} day^{-2}	0.01-1×10-3	Thornley (2001); Eckertsten et al.(2006); Corre-Hellou et al. (2007); Corre-Hellou et al. (2009);
ft	soil temperature factor	°C		
t_min	the minimum temperature for the start of N fixation	°C	0.5~5	Boote et al. (2008)
t_max	the maximum temperature for the stop of N fixation	°C	40~45	Boote et al. (2008)
t_optL	lower bond of optimal temperature	°C	10~20	Boote et al. (2008)
t_optH	upper bond of optimal temperature	°C	25~35	Boote et al. (2008)
fw	soil water factor			
φ1	coefficient for soil moisture		0	
φ2	coefficient for soil moisture		2	APSIM, EPIC (Sharpley and Williams, 1990; Bouniols et al., 1991; Cabelguenne et al., 1999); SOILN (Wu and McGechan, 1999)
Wa	lower bond of water content below which N fixation is totally restrict by rhe defict of soil water		0	APSIM, EPIC (Sharpley and Williams, 1990; Bouniols et al., 1991; Cabelguenne et al., 1999); SOILN (Wu and McGechan, 1999)
Wb	upper bond of water content above which N fixation is not limited by the defict of soil water		0.5	APSIM, EPIC (Sharpley and Williams, 1990; Bouniols et al., 1991; Cabelguenne et al., 1999); SOILN (Wu and McGechan, 1999)
Wf	available soil water content to that at field capacity			
f_Nup	parameter relating legume biological nitrogen fixation and soil nitrogen content		0.01~0.1	SOILN model (Wu and McGehan, 1999)
Ns	Soil mineral nitrogen content	g N m^{-2}		
f_N	Soil mineral N effect			
f_C	Soil carbon effect			
Cr	Carbon concentration in the soil	g C g^{-1} soil		
Kc	Michaelis-Menten Constant for carbon	g C g^{-1} soil	0.001~0.01	Thornley (2001); Eckertsten et al. (2006)

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Table 2. Calibration Sites of Biological Nitrogen Fixation Rate for Representative Ecosystems

Site name	Ecosystem Type	Lon.	Lat.	Experimental method	Reference	N Fixation Rate kg N ha⁻¹ yr⁻¹	Simulation, kg N ha⁻¹ yr⁻¹
Stordalen, Sweden	Tundra	18	68	ARA	Christie (1987); Sonesson et al. (1980)	2	2.5
Truelove Lowland, Canada	Tundra	-84.5	75.5	ARA	Chapin et al. (1990)	3	2.8
Niwot Ridge, Colorado, US	Tundra	-105.5	40	¹⁵N	Bowman et al. (1996)	4.9	5.1
Central Sweden	Boreal Forest	18	60	ARA	Nohrstedt (1985)	0.93	0.9
PNFI, Ontario, Canada	Boreal Forest	-77	45.5	ARA	Hendrickson (1990)	0.25	1.2
Southern British Columbia, Canada	Boreal Forest	-119	49	ARA	Hendrickson and Burgess (1989)	2.8	2.2
Robson moralines, British Columbia	Boreal Forest	-119	53	ARA	Blundon and Dale (1990)	1.1	1.2
Umea, Sweden	Boreal Forest	19.5	64	ARA	Huss-Danell (1976)	1	1.5
Coweeta Basin,	Temperate Forest	-83	35	N accumulation	Boring and Swank (1984)	48	19.5
Hoh River, Washington, US	Temperate Forest	-123.5	48	ARA	Luken and Fonda (1983)	40	13
Tom Swamp, Massachusetts, US	Temperate Forest	-75	42.5	unspecified	Schwinzer (1983)	35	25.7
Big Creek Basin, Melbourne, Austrilia	Temperate Forest	145.5	38	ARA	Adams and Attiwill (1984)	24	23.2
Jebo Creek, Utah, US	Temperate Forest	-112	42	¹⁵N	Skujins et al. (1987)	10.2	12.5
Karri Forest, south-western Austrilia	Temperate Forest	116	-34.5	ARA	Grove and Malajczuk (1992)	7.93	8.5
Woodhill Forest, New Zealand	Temperate Forest	174.5	-37	N accumulation	Baker et al. (1986)	80	23.5
Gainesville, Florida, US	Temperate Forest	-82	30	N accumulation	Permar and Fisher (1983)	10.6	12.8
Fox park, Wyoming, US	Temperate Forest	-106	41	ARA	Fahey et al. (1985)	13	12.5
Mount Robson, Canada	Temperate Forest	-119	53.1	ARA	Blurdon and Dale (1990)	1.65	3.2
Dwellingup, South-western Austrilia	Temperate Forest	116	33	ARA	OConnel and Grove (1987)	2.5	3.1
Adair, Oregon, US	Temperate Forest	-123	44.6	ARA	Heath et al (1988)	0.74	2.4

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Location	Biome			Method	Reference		
Priest River Experimental Forestry, Idaho, US	Temperate Forest	-116	48	ARA	Harvey et al (1989)	0.1	1.7
Arapaho Prarie, Nebraska, US	Grassland	-100	42	unspecified	Kaputsa and DuBois (1987)	0.2	0.7
Lynx Prairie Preserve, Ohio, US	Grassland	-83.5	39	ARA	DuBois and Kaputsa(1983)	8.2	1.9
Konza Prarie Research Natural Area, Kansas, US	Grassland	-96	39.5	nitrogenase activity	Eisele et al (1989)	21	3.3
Buso, Papua New Guinea	Tropical Forest	147	-7.5	ARA	Goosem and Lamb (1986)	0.5	5.2
Reserve Ducke, Manaus, Brazil	Tropical Forest	-59	-3	ARA	Sylvester-Bradley et al. (1980)	2.45	3.5
Sinharaja Man and Biosphere reserve	Tropical Forest	80.5	6.5	ARA	Maheswaran and Gunatilleke (1990)	8	8.5
Amazon Territory of Venezuela	Tropical Forest	-67	2	ARA	Jordan et al (1983)	32	20.3
Kilauea, Hawaii, US	Tropical Forest	-155	19	ARA	Vitousek (1994)	2.8	18.5
Volcano La Soufriere, Guadeloupe	Tropical Forest	-61.5	16	ARA	Sheridan (1991)	4.02	7.2
Hawaii Volcanoes National Park, US	Tropical Forest	-155	19.5	ARA	Ley and D'Antonio (1998)	4.9	9.3
Santa Ynez Mountain, California, US	Mediterranean Shrubland	-120	34.5	ARA	Schlesinger et al.(1982)	1	2.4
San Bernardino Mountains, California, US	Mediterranean Shrubland	-116.5	34	ARA	Lepper and Fleschner (1977)	6.9	3.7
Harpers Well, California, US	Xeric Shrubland	-116	33.5	N accumulation	Rundel et al.(1982)	30	18.5
Sonoran Desert, Arizona, US	Xeric Shrubland	-112.5	33	cation accumulation	Jarrell and Virginia (1990)	40	23.5

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Table 3. Sites used for model validation of N$_2$O emissions

Site name	Ecosystem Type	Lon.	Lat.	T (°C)	Precipitation (mm)	Length of experiment (day)	N$_2$O Fluxes kg N ha^{-1} yr^{-1}	Reference
Linden, Giessen,	Temperate							Müller and Shelock
1 Germany	forest	8.5	50.5	1~20	0-14	400	0.292	(2004)
2 Horquetas, Costa Rica	Savanna	-85	10	25.8	3962	23-30	4.3	Veldkamp et al. (1998)
3 Yurimaguas, Peru	Rainforest	-76	-6	26	2200	365	0.8	Palm et al. (2002)
4 Central Scotland	Grassland	-4.5	56.5	12.6	129.3	7	0.02-0.09	Skiba et al. (1998)
5 Wagga Wagga	Grassland	147.5	-35.5	3~31	570	90	0.35	Galbally et al. (2009)

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Table 4. Model estimated biological nitrogen fixation in global natural terrestrial ecosystems

Ecosystem	Average coverage of N fixing plants	Coverage range	Reference	N Fixation Rate (kg N ha^{-1} yr^{-1})	Total_Min (Tg N yr^{-1})	Total_Max (Tg N yr^{-1})	Total_Avg (Tg N yr^{-1})	Area (10^8 ha)
wet tundra	9%	3%~15%	May and Webber (1982)	3.2	0.51	2.55	1.54	5.37
alpine tundra & wet tundra	9%	3%~15%	May and Webber (1982)	3.2	0.51	2.55	1.54	5.36
boreal forest	9%	4%~18%	Alexander and Billington (1986); weber and Van Cleve (1981)	2.1	2.01	9.06	4.53	19.3
temperate coniferous forest	5%	1%~10%	Cleveland et al (1999)	12.7	0.71	7.15	3.5	5.51
temperate deciduous forest	5%	1%~10%	Cleveland et al 1999	12.7	0.76	7.65	3.75	5.89
temperate evergreen forest	5%	1%~10%	Cleveland et al (1999)	12.7	0.43	4.34	2.13	3.35
grassland	15%	5%~25%	Woodmansee et al (1981); Robertson and Rosswall (1986)	1.9	0.61	3.1	1.86	8.4
tropical forest	15%	5%~25%	Cleveland et al (2001)	18.2	10.8	54	32.6	17.8
xeric shrubland	15%	10%~20%	Johnson and Mayeux (1990)	5.7	2.92	14.6	8.35	14.8
Mediterranean shrubland	15%	10%~20%	Johnson and Mayeux (1990)	2.7	0.13	0.66	0.4	1.47
savanna	15%	5%~25%	Stewart et al (1978); Bate and Gunton (1982)	1.9	0.45	2.23	1.34	7.05
Total					19.84	107.89	61.54	94.3

Table 5. Model parameters for various natural terrestrial ecosystems

		N _pot (g N fixed day $^{-1}$)	t_optL (°C)	t_optH (°C)	W_upH (J kg $^{-1}$)	fNup	Kc (g C m^{-2})
1	wet tundra	0.028	10	25	0.8	65	0.002
2	alpine tundra & wet tundra	0.028	10	25	0.8	65	0.002
3	boreal forest	0.032	12	25	0.8	70	0.008
4	temperate coniferous forest	0.55	16	35	0.6	80	0.01
5	temperate deciduous forest	0.55	18	35	0.6	80	0.01
6	temperate evergreen forest	0.55	18	35	0.6	80	0.01
7	grassland	0.05	18	35	0.5	60	0.012
8	tropical forest	0.8	20	35	0.8	100	0.005
9	xeric shrubland	0.7	15	35	0.4	65	0.016
10	Mediterranean shrubland	0.08	19	35	0.5	65	0.016
11	savanna	0.05	20	35	0.5	60	0.012
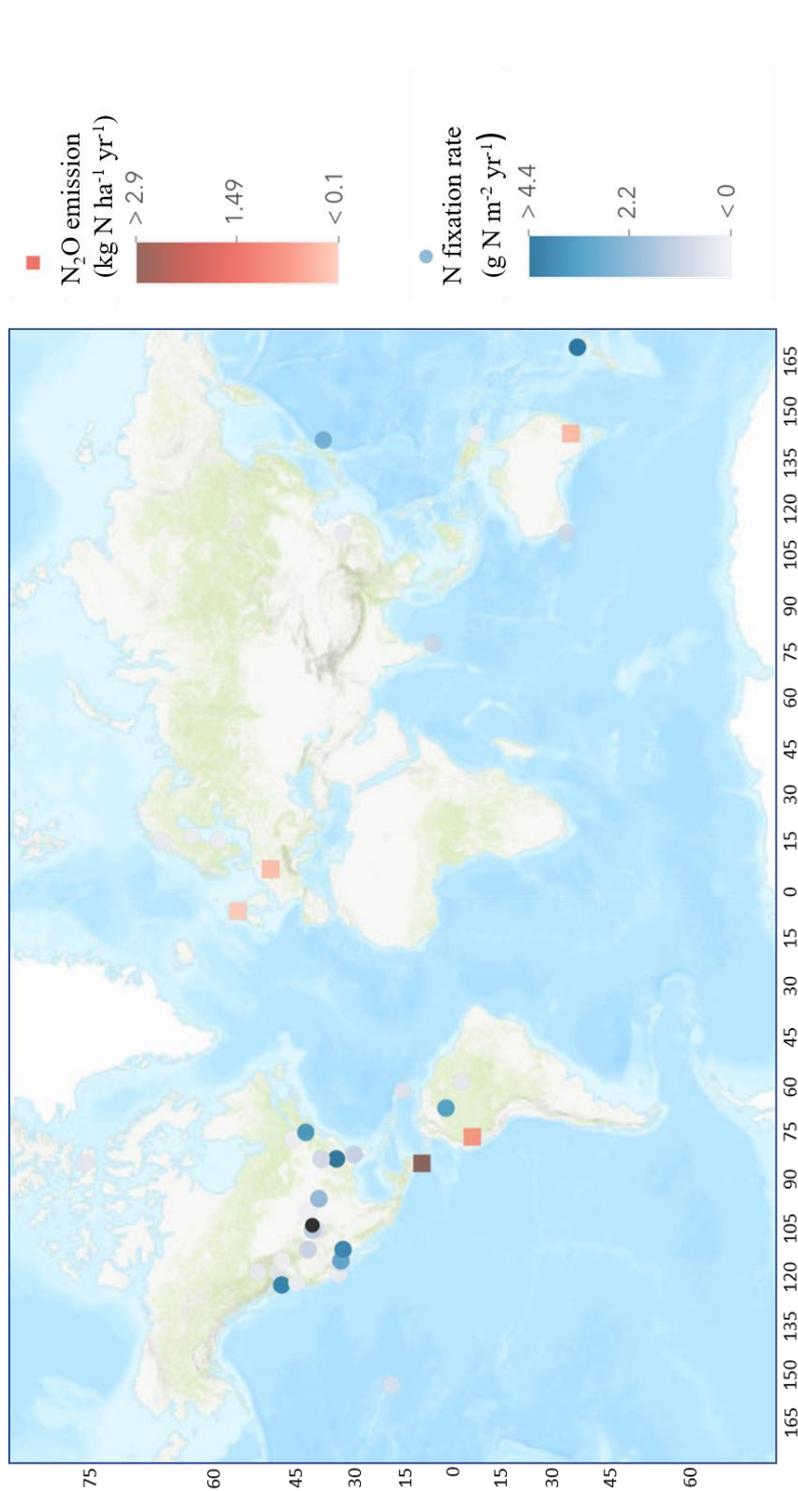
Figure 1. Sites used with observation data of N_2 fixation rate (Blue) and N_2O emissions (Red) for model parameterization
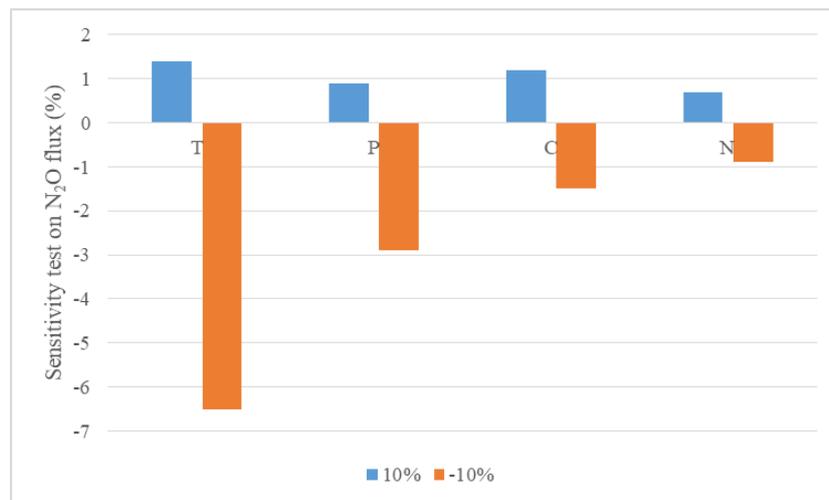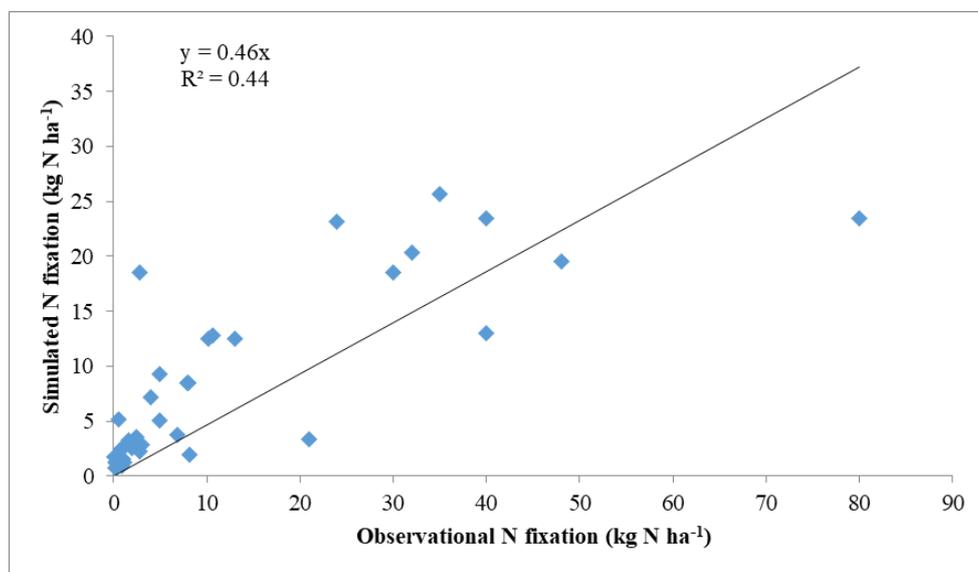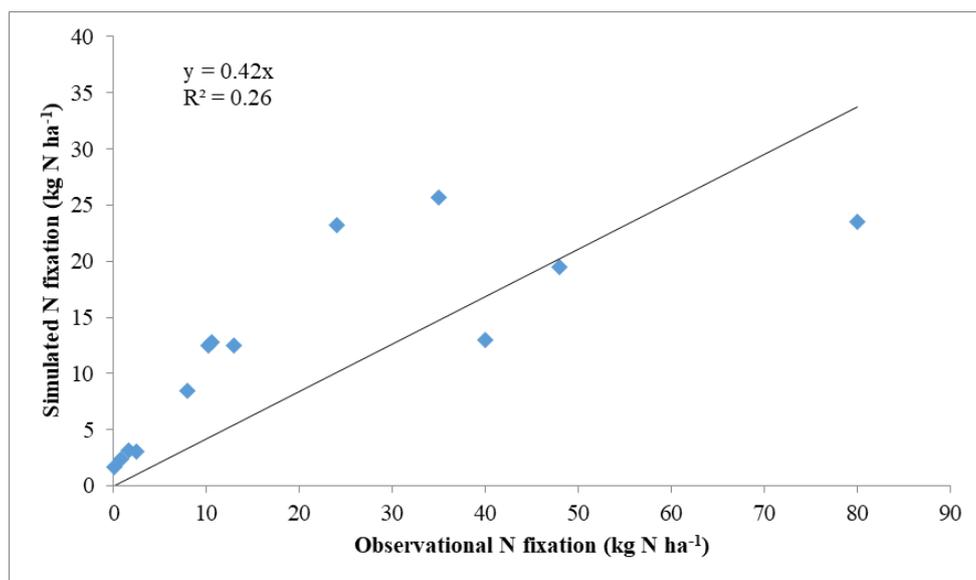
(a)
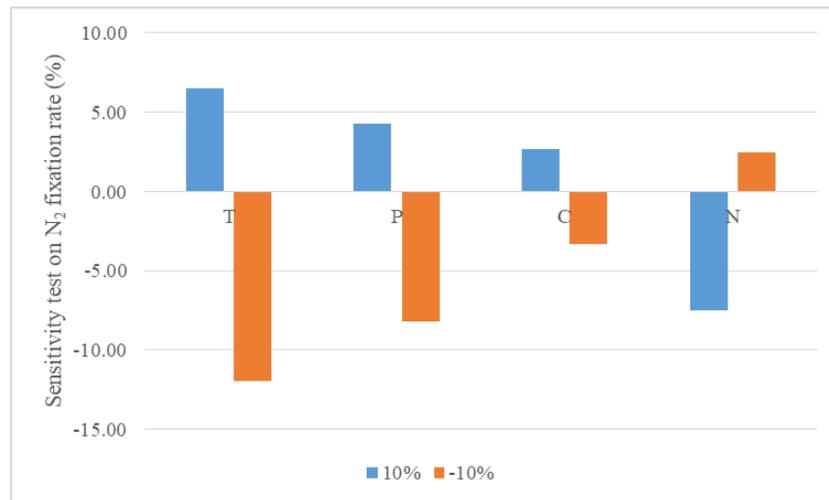
(b)

Figure 2. Model sensitivity of N fixation and N_2O emissions in natural terrestrial ecosystems to changing model input data: Increasing or decreasing each variable by 10% for air temperature (T), precipitation (P), soil carbon content (C), soil nitrogen content (N) for (a) N fixation rate and (b) N_2O emissions
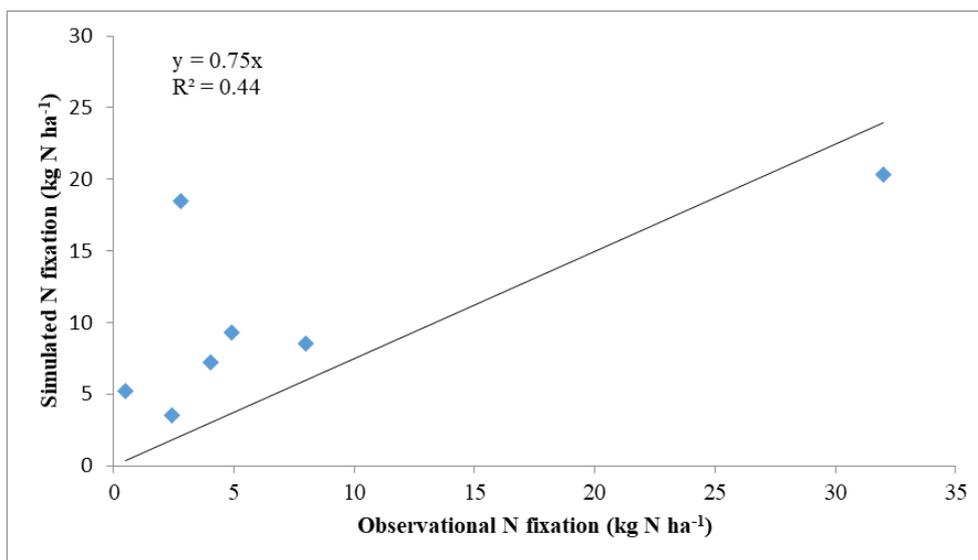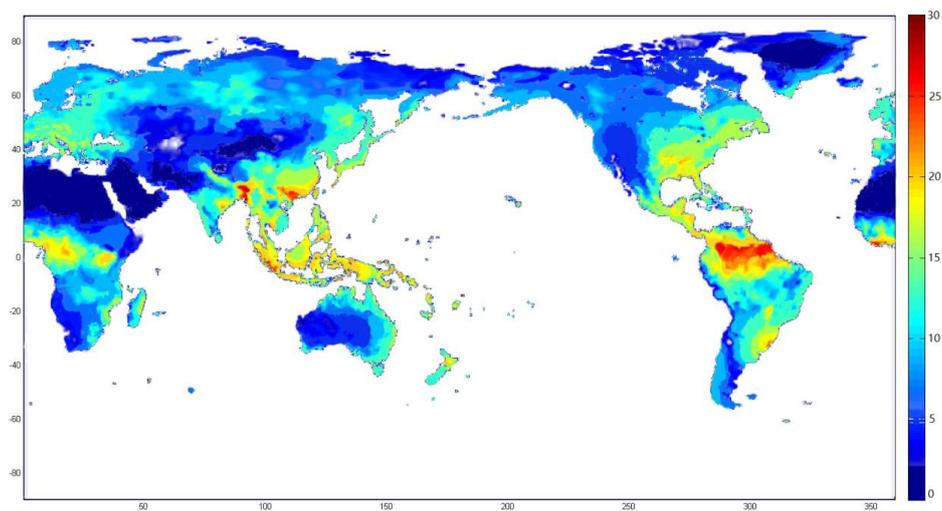
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(a)

(b)

(c)

Figure 3. Comparison between Modeled and Observed Nitrogen Fixation Rate at site level: (a) All sites, (b) Temperate Forest, (c) Tropical Forest (data listed in Table 2). Y is simulated N fixation while X represents the observational N fixation.

(a)

(b)
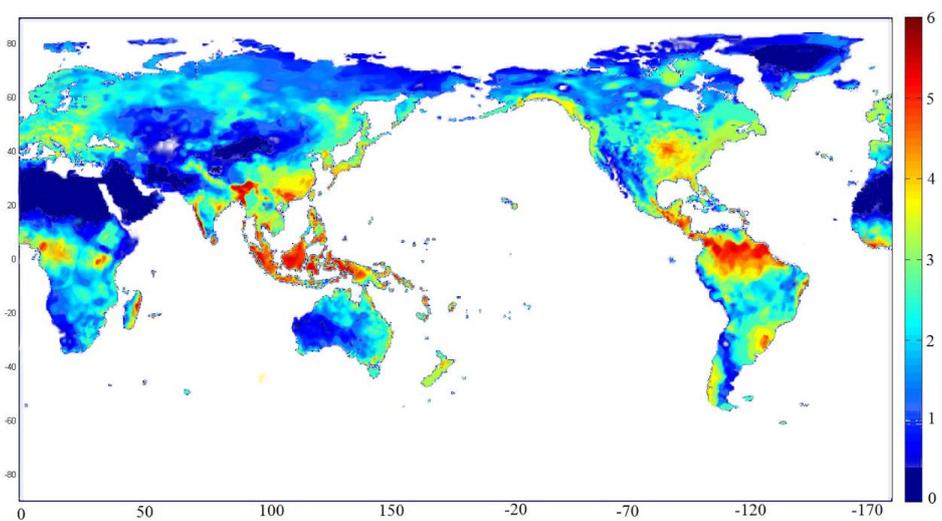
Figure 4. Simulated spatial distribution of (a) BNF rates (kg N ha^{-1} yr^{-1}); (b) N$_2$O emissions (kg N ha^{-1} yr^{-1}) in natural terrestrial ecosystems during 1990-2000 by considering the BNF effects.
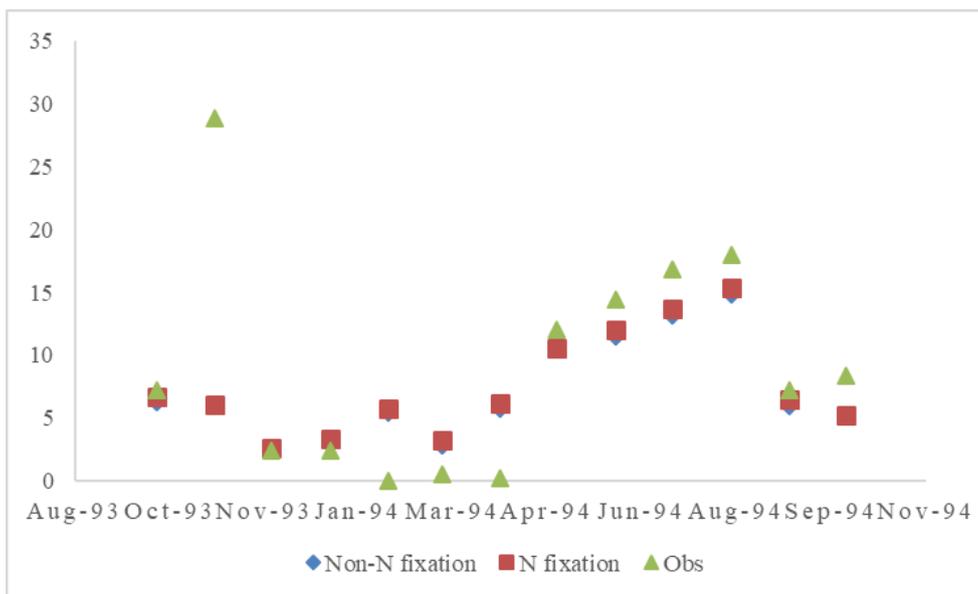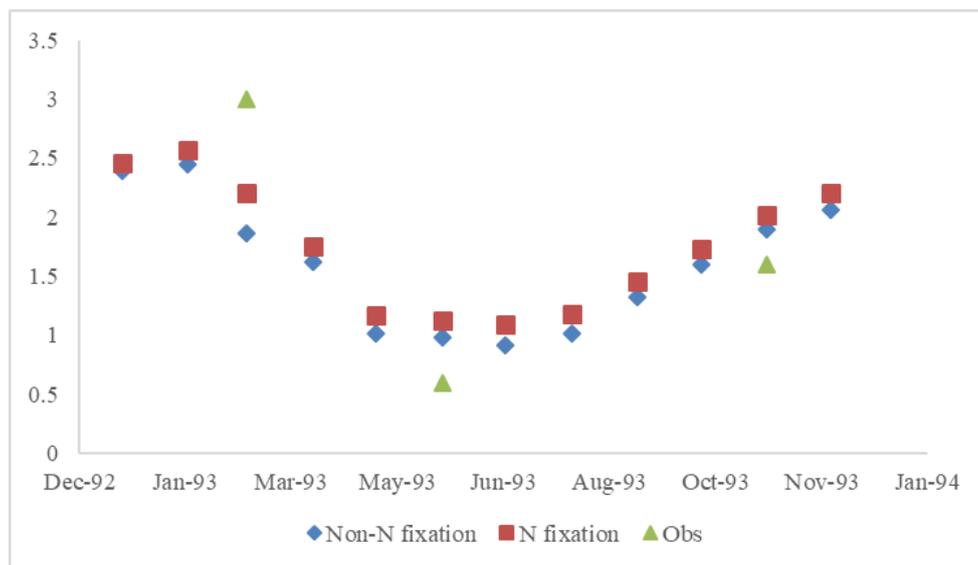
(a)
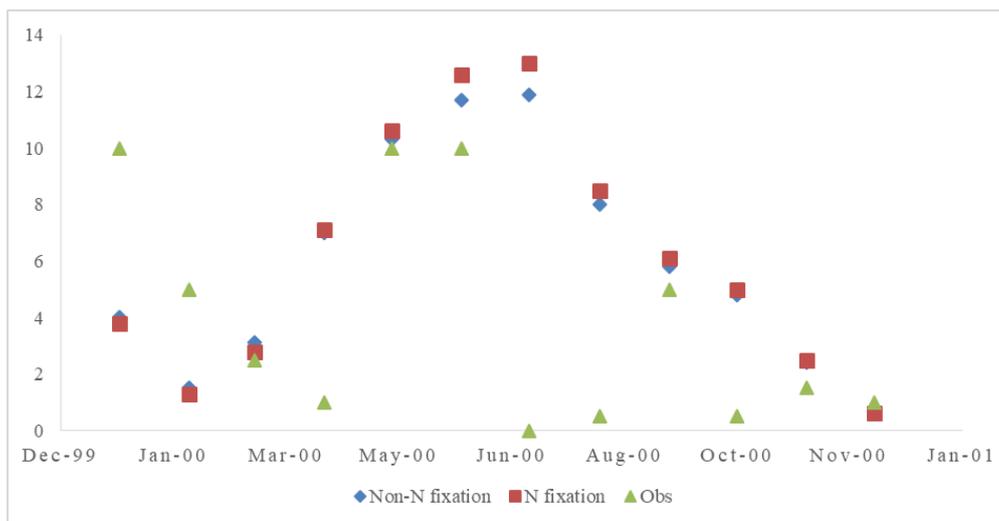
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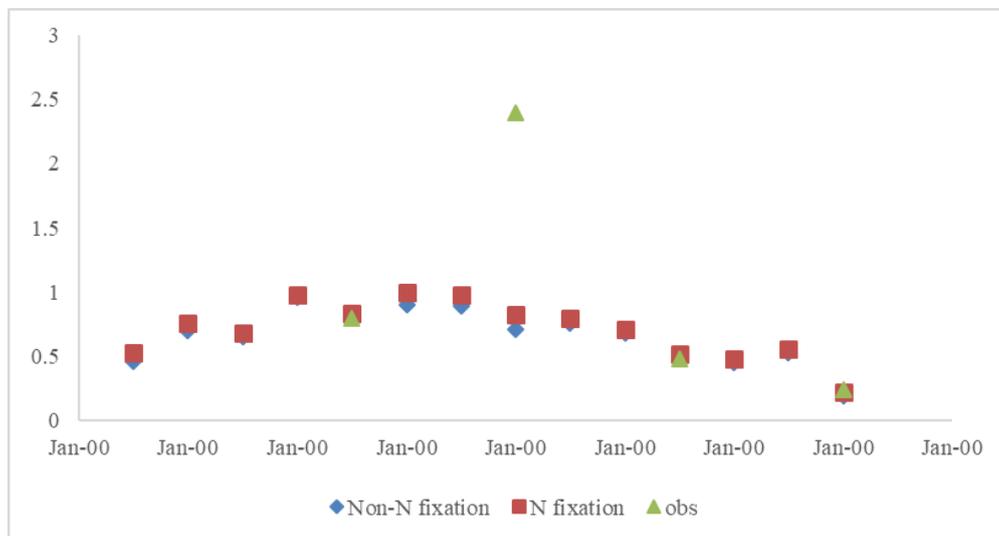
(c)
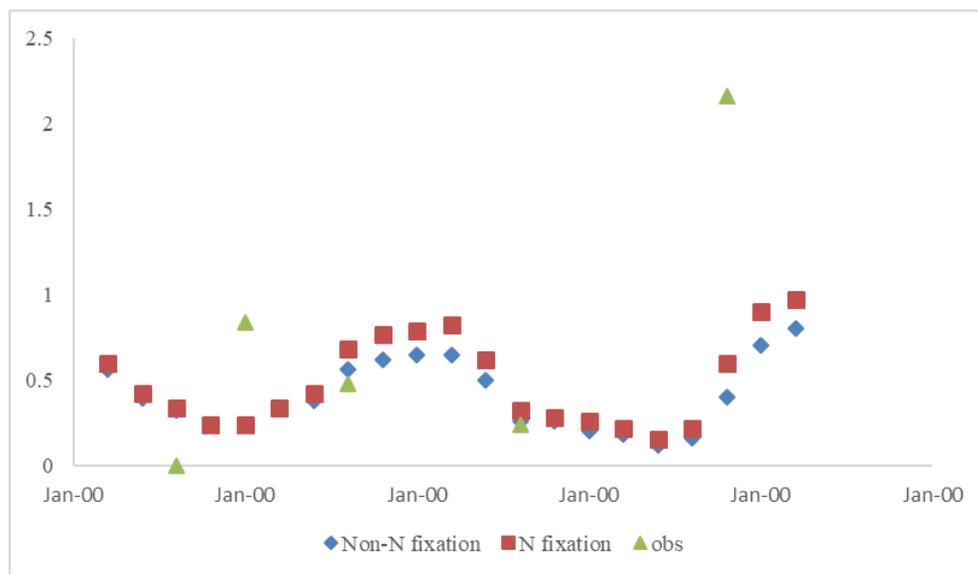
(d)

(e)

Figure 5. Comparison between simulated and observed N_2O emissions (g N m^{-2} day^{-1}) with two versions of the model (Red indicates the simulations considering BNF and blue indicates the simulations without considering BNF effects on N_2O emissions) at sites: (a) Temperate Forest (50.5°N, 8.5°E); (b) Tropical Forest (10°S, 63°W); (c) Savanna (10°N, 85°W); (d) Tropical Forest (6°S, 76°W).