



Modeling biological nitrogen fixation in global natural terrestrial ecosystems

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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, process-based models are needed. This study develops a biological nitrogen fixation model to quantitatively estimate the nitrogen fixation rate by plants in a natural environment. The revised nitrogen module better simulates the nitrogen cycle 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, which decreases from the Equator to the polar region. The estimated nitrogen fixation in global terrestrial ecosystems is $61.5 \text{ Tg N yr}^{-1}$ with a range of $19.8\text{--}107.9 \text{ Tg N yr}^{-1}$ 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, the contribution of nitrogen made by biological nitrogen fixation depends on ecosystem type and climatic conditions. This study highlights that there are relatively large effects of biological nitrogen fixation on ecosystem nitrogen cycling, and the large uncertainty of the estimation calls for more comprehensive understanding of biological nitrogen fixation. More direct observational data for different ecosystems are in need to improve future quantification of 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). Nitrogen usually enters terrestrial ecosystems through processes of nitrogen deposition and from biological N fixation (BNF). Nitrogen deposition is a physical process, representing the direct input of reactive nitrogen including 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 $3\text{--}5 \text{ Tg N yr}^{-1}$ to terrestrial ecosystems (Levy and Moxim, 1996). Nitrogen input via rock weathering is another important source for terrestrial ecosystems, adding $3\text{--}10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Morford et al., 2011; Houlton et al., 2018). BNF is significantly greater than lightning-induced N fixation (Galloway et al., 1995). On a global scale, anthropogenic nitrogen in the environment could be more than 160 Tg N yr^{-1} (Gruber and Galloway, 2008), which is even greater than terrestrial N fixation ($\sim 110 \text{ Tg N yr}^{-1}$). However, taken together, natural N fixation is the primary source of global terrestrial ecosystems in the absence of human activities. 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_2 fixation generally affects the nitrogen cycle and nutrient level to constrain plant productivity. Any change in nitrogen input to terrestrial ecosystems will influence their soil nitrogen content.

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 a natural environment, N_2 fixation is conducted by two types of microorganisms: asymbiotic organisms and symbiotic organisms. The former includes blue-green algae, lichens and free-living soil bacteria (Belnap, 2002; Granhall and Lid-Torsvik, 1975), and the later includes fungi and nodule-forming *Rhizobium* species. Among them, the most dominant fixers are leguminous plants, and their N fixation mechanisms are also the best known (Sullivan et al., 2014; Vitousek et al., 2013). A symbiotic relationship exists between legume plants and bacteria, in which legume plants provide the bacteria with energy through photosynthesis, and the bacteria around the rhizobia supply the legume with N in the form of ammonia. To date, the amount of N fixation by legumes is estimated to be 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.

The biological N_2 fixation rate has been usually measured or estimated at a particular observational site. To quantify the fixation amount at the global scale, process-based models and sufficient observational data are needed. This study develops a BNF model considering the symbiotic relationship between legume plants and bacteria. The model is extensively calibrated with site-level observational data. The model is then extrapolated to the global terrestrial ecosystems to quantify the fixation rate in the 1990s. The factors influencing the fixation rate are also analyzed for different terrestrial ecosystems, including the distribution of legume plants, soil temperature, and soil properties and types.

2 Methods

2.1 Overview

We first develop a BNF model and then couple the model with an earlier version of a biogeochemistry model quantifying soil carbon and nitrogen dynamics (Yu and Zhuang, 2019). The revised model is then used to quantify the BNF at regional and global scales in 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 modified model is calibrated and evaluated with observed N_2 fixation rate data from published studies for various 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 time step and a spatial resolution of 0.5° by 0.5° for

the final decade of the 20th century. The effects of physical conditions on BNF are then analyzed.

2.2 Model description

The Terrestrial Ecosystem Model (TEM) is a process-based model that simulates carbon and nitrogen dynamics and 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_2 fixation by legumes. The model schematic and other calculations including the carbon cycle and the nitrogen cycle 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_2 fixers could exist 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 croplands and seminatural environments (Mus et al., 2016). In natural environments, contributions from legumes can be significant but with large uncertainties, which is greatly determined by various environmental conditions (Lindemann and Glover, 1996). In this study, the N_2 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_2 fixation and (5) the percentage of N_2 fixing plants for each ecosystem type as

$$N_{\text{fix}} = N_{\text{fixpot}} f_t f_w f_N f_C f_{\text{plant}}, \quad (1)$$

where N_{fix} is the nitrogen fixation rate, N_{fixpot} is the potential N_2 fixation rate (g N d⁻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. Please refer to Table 4 for the value range of related parameters.

The potential N_2 fixation is highly related to the total N demand of plants and the available nitrogen in soils. Theoretically, the definition of the potential N_2 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_2 fixation because of data availability. N_{fixpot} can be estimated based on 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 using an acetylene reduction array (ARA) method (Hardy et al, 1968, 1973), and some researchers used

¹⁵N 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 the 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 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, the relation between the factor and temperature is not exactly a Gaussian distribution. BNF increases as the temperature rises from a minimum temperature (0–5 °C) for N fixation to the optimal temperature; the maximum rate occurs within an optimal range (15–25 °C) and decreases from the optimal to the maximum temperature, above which BNF will stop at 35–40 °C:

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

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 (Wu and McGechan, 1999; Boote et al., 2008; Holzworth et al., 2014) (Table 1). For 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 the nitrogen-fixing system (Sprent, 1972). With proper temperature, the soil moisture condition is the major factor controlling the nitrogen fixation rate (Srivastava and Ambasht, 1994). Soil water deficit and flood dramatically inhibit N_2 fixation because of drought stress and oxygen deficit, respectively (Omari et al., 2004; Marino et al., 2007). In our model, the water factor is linearly related to soil water content (Williams, 1990; Wu and McGachan, 1999):

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

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 typical soils, which has little effect on 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_2 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_2 fixation, respectively (Table 1).

It is generally thought that more substrate N in soils will slow down the N_2 fixation because plants can take up N directly from soil with less energy (Vitousek and Field, 1999). By comparison, N_2 fixation needs more energy and consumes more carbon than plant N uptake does. Thus, the N_2 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 McGechan (1999):

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

where f_{Nup} is a parameter related to legume biological N_2 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.

N_2 fixers get photosynthetic carbohydrate support from plants. Because the product of every unit of nitrogen fixed consumes a certain amount of carbon, the lack of carbon supply will inhibit the N_2 fixation. The carbon cost per unit of fixed N_2 varies widely depending on environmental conditions and ecosystem types. For example, the consumption of carbon is only 1.54 times of fixed N_2 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 Michaelis–Menten equation (Boote et al., 1998):

$$f_C = \frac{1}{1 + K_c/C_r}, \quad (5)$$

where C_r is the soil carbon content ($g\ C\ m^{-2}$) to represent carbon availability from plants to N_2 fixers. K_c is the Michaelis–Menten constant, which is plant species dependent.

2.3 Data

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. Nitrogen fixation rates were determined with the ARA method in most published studies (Table 2; data were from Cleveland et al., 1999), expressed in kilograms of N per square meter per year. Some of them were measured with the ¹⁵N natural abundance technique.

The parameters for the N_2 fixation module were initialized with a priori values (Table 2). Ecosystem-specific and microbe guild-specific parameters were inherited from a previous TEM model (Zhuang et al., 2003; Yu and Zhuang, 2019).

Table 1. Description of parameters used in the model.

Parameters	Description	Unit	Reference value	reference
N_{fix}	nitrogen fixation rate	$g\ N\ m^{-2}\ d^{-1}$		
N_{fixpot}	potential nitrogen fixation rate	$g\ N\ m^{-2}\ d^{-2}$	$0.01-1 \times 10^{-3}$	Thornley (2001), Eckertsten et al. (2006), Corre-Hellou et al. (2007, 2009)
f_t	soil temperature factor	$^{\circ}C$		
t_{min}	the minimum temperature for the start of N fixation	$^{\circ}C$	0.5 ~ 5	Boote et al. (2008)
t_{max}	the maximum temperature for the stop of N fixation	$^{\circ}C$	40 ~ 45	Boote et al. (2008)
t_{optL}	lower threshold of optimal temperature	$^{\circ}C$	10 ~ 20	Boote et al. (2008)
t_{optH}	upper threshold of optimal temperature	$^{\circ}C$	25 ~ 35	Boote et al. (2008)
f_w	soil water factor			
φ_1	coefficient for soil moisture		0	
φ_2	coefficient for soil moisture		2	APSIM, EPIC (Sharpley and Williams, 1990; Bouniols et al., 1991; Cabelguenne et al., 1999); SOILN (Wu and McGechan, 1999)
W_a	lower threshold of water content below which N fixation is totally restricted by the deficit of soil water		0	APSIM, EPIC (Sharpley and Williams, 1990; Bouniols et al., 1991; Cabelguenne et al., 1999); SOILN (Wu and McGechan, 1999)
W_b	upper threshold of water content above which N fixation is not limited by the deficit of soil water		0.5	APSIM, EPIC (Sharpley and Williams, 1990; Bouniols et al., 1991; Cabelguenne et al., 1999); SOILN (Wu and McGechan, 1999)
W_f	ratio of 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 McGechan, 1999)
N_s	soil mineral nitrogen content	$g\ N\ m^{-2}$		
f_N	soil mineral N effect			
f_C	soil carbon effect			
C_r	carbon concentration in the soil	$g\ C\ g^{-1}\ soil$		
K_c	Michaelis–Menten constant for carbon	$g\ C\ m^{-2}$	0.001 ~ 0.01	Thornley (2001), Eckertsten et al. (2006)

Table 2. Calibration sites of biological nitrogen fixation rate for representative ecosystems.

Site name	Ecosystem type	Long	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. (1991)	3	2.8
Niwot Ridge, Colorado, US	Tundra	-105.5	40	¹⁵ N	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
Mount Robson, 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	Lukens and Fonda (1983)	40	13
Tom Swamp, Massachusetts, US	Temperate forest	-75	42.5	Unspecified	Schwintzer (1983)	35	25.7
Big Creek Basin, Melbourne, Australia	Temperate forest	145.5	38	ARA	Adams and Attwill (1984)	24	23.2
Jebo Creek, Utah, US	Temperate forest	-112	42	¹⁵ N	Skujins et al. (1987)	10.2	12.5
Karri Forest, southwestern Australia	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	Blundon and Dale (1990)	1.65	3.2
Dwellingup, southwestern Australia	Temperate forest	116	33	ARA	O'Connell and Grove (1987)	2.5	3.1
Adair, Oregon, US	Temperate forest	-123	44.6	ARA	Heath et al. (1988)	0.74	2.4
Priest River Experimental Forestry, Idaho, US	Temperate forest	-116	48	ARA	Harvey et al. (1989)	0.1	1.7
Arapaho Prairie, Nebraska, US	Grassland	-100	42	Unspecified	Kapustka 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 Prairie 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
La Grande Soufrière, 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

* ARA denotes the acetylene reduction assay method in determining biological N₂ fixation rates.

The global simulations were conducted at a spatial resolution of 0.5 by 0.5° 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 contents were from Chen and Zhuang (2013) and Zhuang et al. (2012).

For regional simulations, the total amount of fixed N₂ was also influenced by legume coverage. For each ecosystem type, we estimated the coverage according to the distribution of legume plants and field studies (Table 3; the coverage data are compiled from Cleveland et al., 1999), where the minimum and maximum values were derived from the abundance of N₂ fixers.

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 seven 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 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 the nitrogen cycle in the soil have been defined and calibrated in previous studies (Yu and Zhuang, 2019). The calibrated model is evaluated at the site level and then extrapolated to the global terrestrial ecosystems.

2.5 Model sensitivity and uncertainty analysis

The response of N₂ fixation of different biomes to input data and variation in parameters was analyzed using sensitivity testing. 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 $\pm 10\%$ of the original level for each site and each grid. The variables were changed at six levels, and the rest of the input variables were kept at their original values. The sensitivity was calculated by comparing the simulated annual nitrogen fixation to the simulations with the original input values.

3 Results

3.1 Model evaluation

To evaluate the model, 35 observational sites were selected for seven major ecosystem types across the globe, representing different climate and soil conditions. The experimental

Table 3. Model estimated biological nitrogen fixation in global natural terrestrial ecosystems.

Ecosystem	Average coverage of N ₂ fixing plants	Coverage range	Reference	N ₂ fixation rate (kg N ha ⁻¹ yr ⁻¹)	TotalMin (Tg N yr ⁻¹)	TotalMax (Tg N yr ⁻¹)	TotalAvg (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 and 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. (2010)	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 4. Model parameters for various natural terrestrial ecosystems.

		N_{pot} (g N ₂ fixed d ⁻¹)	t_{optL} (°C)	t_{optH} (°C)	W_{upH} (J kg ⁻¹)	f_{Nup}	K_c (g C m ⁻²)
1.	Wet tundra	0.028	10	25	0.8	65	0.002
2.	Alpine tundra and 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

data of N₂ fixation have a mean value of 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 a temperate forest in New Zealand, while the minimum rate was also for a temperate forest in the state of Idaho in 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 (Fig. 2). The regression results are mainly influenced by some observed data greater than 30 kg N ha⁻¹ yr⁻¹. By removing the outliers of observational data, the slope of 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 the minimum one. Simulations are closer to the observations across sites in temperate forests with R^2 of 0.26 and a slope of 0.42. Our model underestimated a 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. For tropical forests, our model estimates of N₂ fixation are higher than observations with a slope of 0.75 and R^2 of 0.44.

3.2 Model sensitivity analysis

The model sensitivity analysis quantifies the impact of changes in forcing data on nitrogen fixation rate. Climate conditions including air temperature and precipitation and soil characteristics of nitrogen content and carbon content varied at three levels to examine the sensitivity. The response of nitrogen fixation rate emissions is quantified for each ecosystem type. The sensitivity test was conducted for all observational sites (Table 2). Temperature is the most sensitive variable (Fig. 1). Nitrogen fixation is more sensitive to the change in all forcing conditions. Increasing soil nitrogen results in a lower N₂ fixation. Abundant soil nitrogen content inhibits BNF activity but stimulates nitrification and denitrification processes.

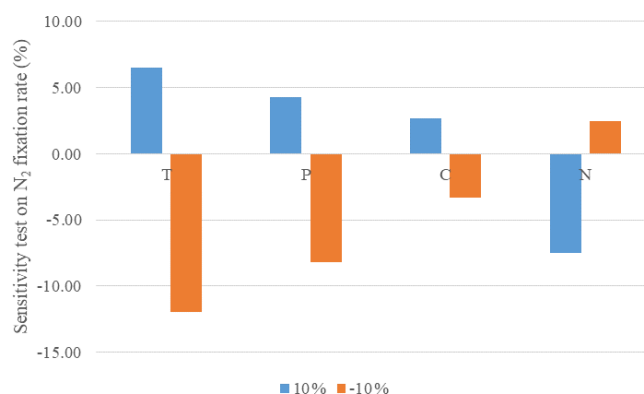


Figure 1. Model sensitivity of N₂ fixation in natural terrestrial ecosystems to changing model input data: increasing or decreasing each variable by 10% for air temperature (T), precipitation (P), soil carbon content (C) and soil nitrogen content (N) for N₂ fixation rate.

3.3 Biological nitrogen fixation in global terrestrial ecosystems

Tropical forests in South America, Central Africa and South Asia show a wide range of N₂ fixation rates 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 one set of parameters is 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 N₂ 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 to 54 Tg N yr⁻¹, with an average value of 32.5 Tg N yr⁻¹ (Table 3). Nitrogen fixation in tropical forests is almost half of the global total amount and a principal contributor of BNF in natural ecosystems. 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 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. Compared to other ecosystem types in temperate regions, conifers are likely to limit the reproduction of legumes (Wheatley et al., 2009). 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 N₂ 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 3). Nitrogen fixation in temperate areas contributes 12.5% of the global total amount.

Savanna covers over a half of the 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, may legumes significantly contribute to the increase in soil nitrogen (Cech et al., 2008). On average, 15% of the vegetation in the savanna is regarded as legume grass, and biological nitrogen fixation occurs when precipitation is greater than 10 mm per month. Generally, nitrogen fixation in the savanna is restricted by soil moisture, while temperate grassland is limited by both temperature and soil moisture (Bustamante et al., 2006). 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 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 the 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. The nitrogen fixation rate is extremely variable for boreal ecosystems. For tundra, the coverage was 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 an 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.

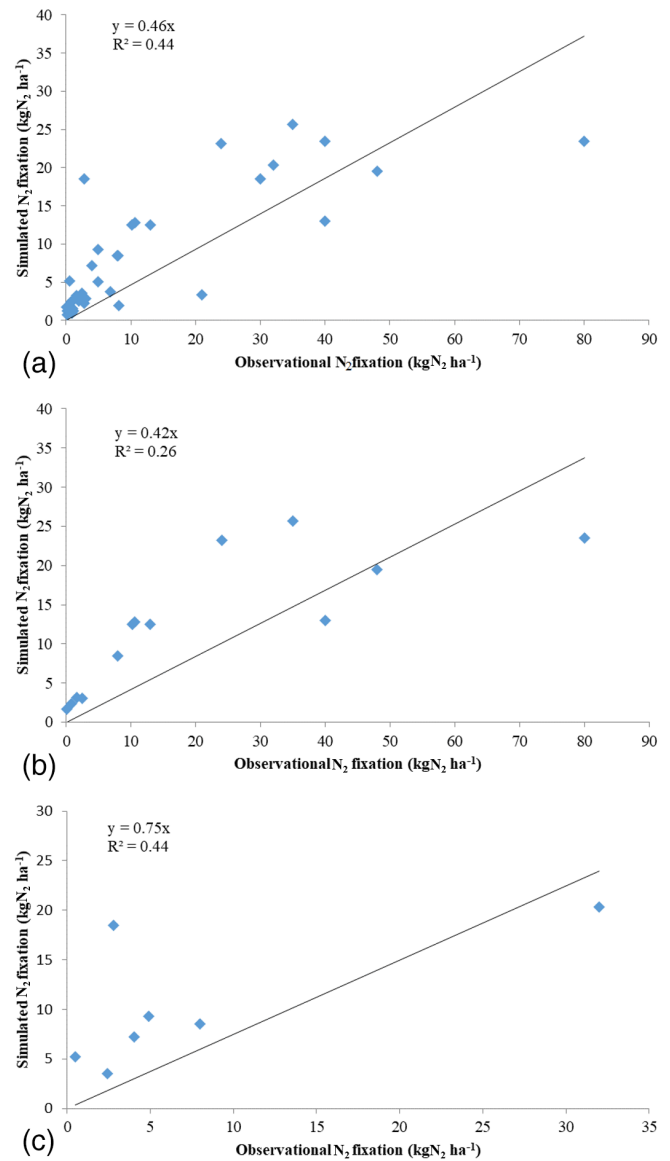


Figure 2. Comparison between modeled and observed nitrogen fixation rate at site level: (a) all sites, (b) temperate forest, (c) tropical forest (data listed in Table 2). The y axis is simulated N₂ fixation, while x represents the observational N₂ fixation.

The fixation could be neglected in deserts because of the extremely dry conditions. Only few legumes may exist in deserts, and their growth is highly depended on precipitation events. Even in semiarid areas, the N₂ fixation rate is much lower than that in tropical and temperate forests (5.7 kg N ha⁻¹ yr⁻¹).

Mediterranean ecosystems such as in southern California and some areas in southern 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 a comparatively wet season than in a dry season

(Sánchez-Díaz, 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_2 fixation rate of these legume species is similar to that in grasslands ($2.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$).

Spatially, the highest rate of N_2 fixation occurred in the tropical and subtropical areas, as a result of proper climate and soil characteristics for fixers (Fig. 3). N fixation from tropical forests and xeric shrubland contributes to nearly half of the global terrestrial amount (Table 3). A lower N_2 fixation rate was found in high latitudes of eastern China, North America and Europe, which were mainly covered with temperate forests. Compared to tropical areas, N_2 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 in humidity and temperature conditions. N_2 fixation in temperate regions accounts for 35 % of the total fixed N_2 .

Our model estimated that high BNF rates in the growing season are 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° (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 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.

From 1990 to 2000, our simulations show that BNF in natural terrestrial ecosystems is $61.5 \text{ Tg N yr}^{-1}$, but anthropogenic N_2 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.

4 Discussion

4.1 Comparison with other estimates of biological nitrogen fixation (BNF)

There is a large uncertainty in estimating the N input into terrestrial ecosystems, especially from BNF (Sutton et al., 2014) (Table 3). In our study, a calibrated process-based model was applied to estimate site-level and global BNF in natural terrestrial ecosystems. Empirical models provide a reasonable estimation based on relationships between N_2 fixation rates and environmental factors (e.g., evapotranspiration) (Cleveland et al., 1999), while process-based approaches consider processes in BNF affected by multiple control-

ling factors (Fisher et al., 2010; Gerber et al., 2008; Gerber et al., 2010). Our estimated BNF in the global terrestrial ecosystems is $61.5 \text{ Tg N yr}^{-1}$ with an uncertainty ranging from 19.8 to $107.9 \text{ Tg N yr}^{-1}$, 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 $100\text{--}289 \text{ Tg N yr}^{-1}$. This range represents potential distribution of nitrogen fixation. In reality, N_2 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 $127.5 \text{ Tg N yr}^{-1}$ 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 $100\text{--}290 \text{ Tg N yr}^{-1}$ and implied that the true rate of BNF would 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 $89\text{--}100 \text{ Tg N yr}^{-1}$. 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 $40\text{--}100 \text{ Tg N yr}^{-1}$, which is similar to our estimates. However, Xu-Ri and Prentice (2017) estimated that the N_2 fixation was about 340 Tg N yr^{-1} , which is almost 5 times larger than our estimates. In their study, BNF was determined by the plant N requirement across all biome types.

In our estimation, tropical forests significantly contribute to the total BNF, which is up to $18 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. 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 ($5.5\text{--}16 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and deciduous forests ($7.5\text{--}30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) (Reed et al., 2011). Barron et al. (2010) directly measured N_2 -fixing root nodules across lowland tropical forests, and their observations also showed large variation among individual trees. For a mature forest matrix, the average value was around $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, but it could be as high as $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for some areas. Cleveland (2013) provided a similar estimate to ours (around $12 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) but higher values ($20\text{--}30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) in their earlier studies (Cleveland et al., 1999). Sullivan et al. (2014) analyzed humans' impact on tropical N fixation and, depending on forest ages, found that fixation was $5.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ with a range from 1.2 to $14.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, which is lower than our estimates.

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

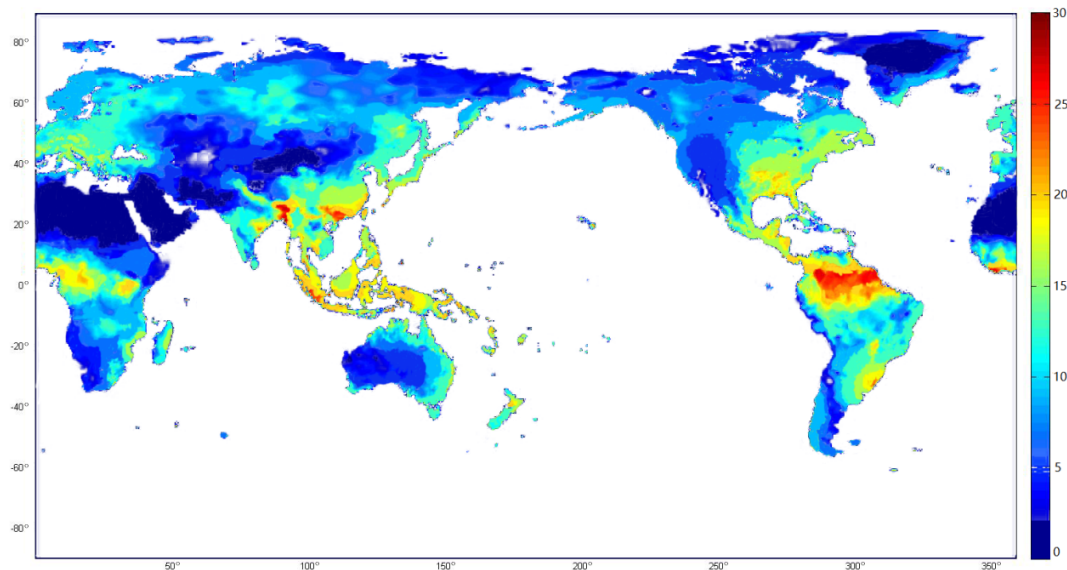


Figure 3. Simulated spatial distribution of BNF rates ($\text{kg N}_2 \text{ ha}^{-1} \text{ yr}^{-1}$) in natural terrestrial ecosystems from 1990 to 2000 by considering the BNF effects.

cyanobacterium and feather moss could act as a supplement to N_2 fixation in boreal forests ($0.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), while the organic N accumulation could be $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. For the forests in the northwest Rocky Mountains, N_2 fixation amount is on average between 0.5 and $2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Clayton and Kennedy, 1985; Fahey et al., 1988), while the model of Kou-Giesbrecht and Menge (2019) estimated the N_2 fixation rate to be $0 - 10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for temperate forests, and 0 to $6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for boreal forests.

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_2 -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_2 fixers is needed, especially in the central Asia, South America and Africa.

Large variations in BNF rates exist across terrestrial ecosystems spatially (Fig. 3). The global BNF spatial pattern is similar to other estimates (Cleveland et al., 1999; Xu-Ri and Prentice, 2017). The highest N_2 fixation rate in tropical regions (more than 50 % of the global terrestrial N_2 fixation) is primarily due to their warm and moist soil conditions. Further, N_2 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 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_2 fixation rate was high in temperate ecosystems but only contributed to 20 % of the total fixation.

4.2 Major controls on biological nitrogen fixation

In our simulations, the N_2 fixation was primarily influenced by soil temperature, moisture and soil nitrogen content. The highest N_2 fixation rate in tropical ecosystems is consistent with our sensitivity analysis for temperature and soil moisture. The sensitivity analysis indicated that a $1 - 3 \text{ }^\circ\text{C}$ increase in temperature led to 7 % increase in N_2 fixation rate. The 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 to temperature. A slight increase in precipitation (10 %) increased the nitrogenase activity. However, the response of N_2 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 global N_2 fixation, while the contribution of boreal forests, with 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_2 fixation rate, which is also 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_2 -fixing plants are still active to compensate for 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. In areas where the energetic cost exceeds 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 a 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 simulate nitrogen cycle from natural 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 seminatural 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 of BNF in 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.

Second, the BNF process in our model is calibrated with a limited amount of data, imposing a general set of parameters on all plant species and soil conditions within an ecosystem type. More observational data from natural terrestrial ecosystems are 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 is human-related (Sobata et al., 2013). As a result, the quality of observational data varies from site to site, and some BNF data are only seminatural. The observational data are imperfect, which might also have biased our estimates through the model parameterization process.

5 Conclusions

This study developed a process-based biological nitrogen fixation model and coupled it with an extant biogeochemistry model. The model was evaluated with observed data for N_2 fixation. The model was then extrapolated to the global natural terrestrial ecosystems. Our model estimates that biological nitrogen fixation in natural terrestrial ecosystems was

$61.5 \text{ Tg N yr}^{-1}$ 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 on N_2 fixation. Lacking the knowledge about the distribution of N_2 fixing plants and their physiological features might have biased our estimates of biological nitrogen fixation at the global scale.

Data availability. 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> (Doherty et al., 1999; Jones, et al., 2012, 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 ORNL gridded soil properties product (https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=546, Batjes, 2000, last access: May 2020) are based on the World Inventory of Soil Emission Potentials (WISE) database (Batjes, 2000). The global average carbon dioxide concentration is observed at NOAA's Mauna Loa Observatory. N deposition data are from the NADP monitor and CAST-NET. 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>, Xu et al., 2014, last access: May 2017). The data presented in this paper can be accessed through our research website (<http://www.eaps.purdue.edu/ebdl/>, last access: May 2017).

Author contributions. QZ and TY designed the research. TY performed model simulations and data analysis. Both authors contributed to paper writing.

Competing interests. The authors declare that they have no conflict of interest.

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