

Global terrestrial nitrogen fixation and its modification by agriculture

<https://doi.org/10.1038/s41586-025-09201-w>

Received: 4 November 2024

Accepted: 27 May 2025

Published online: 16 July 2025



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Biological nitrogen fixation (BNF) is the largest natural source of new nitrogen (N) that supports terrestrial productivity^{1,2}, yet estimates of global terrestrial BNF remain highly uncertain^{3,4}. Here we show that this uncertainty is partly because of sampling bias, as field BNF measurements in natural terrestrial ecosystems occur where N fixers are 17 times more prevalent than their mean abundances worldwide. To correct this bias, we develop new estimates of global terrestrial BNF by upscaling field BNF measurements using spatially explicit abundances of all major biogeochemical N-fixing niches. We find that natural biomes sustain lower BNF, 65 (52–77) Tg N yr⁻¹, than previous empirical bottom-up estimates^{3,4}, with most BNF occurring in tropical forests and drylands. We also find high agricultural BNF in croplands and cultivated pastures, 56 (54–58) Tg N yr⁻¹. Agricultural BNF has increased terrestrial BNF by 64% and total terrestrial N inputs from all sources by 60% over pre-industrial levels. Our results indicate that BNF may impose stronger constraints on the carbon sink in natural terrestrial biomes and represent a larger source of agricultural N than is generally considered in analyses of the global N cycle^{5,6}, with implications for proposed safe operating limits for N use^{7,8}.

The terrestrial biosphere regulates global climate via carbon (C) fixation and storage^{9,10}. Terrestrial C fixation and storage are, in turn, often strongly limited by nitrogen (N) availability^{11,12}. The supply of N from the decomposition of soil organic matter is commonly the dominant source of N to plants. However, soil N supply is frequently lower than plant N demand in natural terrestrial ecosystems¹³. Therefore, additional N inputs from biological N fixation (BNF), atmospheric N deposition and rock weathering are required to overcome this deficit^{1,13}. Previous research suggests that BNF is the primary source of additional N entering natural terrestrial ecosystems each year^{1,13}, supporting 11% of plant N demand and 16% of terrestrial net primary productivity (NPP, the primary metric of C fixation) globally¹³. The capacity for increased NPP in response to CO₂ fertilization and rising temperatures is, therefore, partially dependent on terrestrial BNF^{13,14}. The role of BNF in regulating

N availability and terrestrial C fixation and storage becomes even more relevant in cases where soil N supply declines because of elevated atmospheric CO₂ concentrations and temperatures¹⁵.

Despite the central role of BNF in climate-C cycle feedbacks, estimates of natural terrestrial BNF are highly uncertain^{3,4,16,17}. For instance, whereas global terrestrial NPP estimates since the year 2000 vary about two-fold (from 37 Pg C yr⁻¹ to 84 Pg C yr⁻¹) (ref. 18), estimates of global natural terrestrial BNF over the same timespan vary around eight-fold (from 44 Tg N yr⁻¹ to 340 Tg N yr⁻¹) (refs. 3,4,16,17). Sampling bias has been a persistent source of uncertainty in bottom-up estimates of natural terrestrial BNF, as field measurements of BNF typically occur in areas with abundant N fixers^{3,4}. Previous efforts to adjust for sampling bias at a global scale have relied on a variety of unvalidated upscaling estimates of N fixer abundances^{3,4}. Using a newly compiled BNF dataset¹⁹ and

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Table 1 | Sampling bias in field studies of natural terrestrial BNF

BNF niche	Abundance unit	Mean abundance in BNF studies ^a	Mean abundance from independent global datasets ^a	Ratio of mean abundance in BNF studies compared with independent global datasets
Trees	Relative basal area (%)	79 (n=246)	3 (ref. 30)	26
Shrubs	Ground cover (%)	54 (n=68)	2 (ref. 31)	27
Herbs	Ground cover (%)	59 (n=20)	2 (ref. 31)	30
Dead wood	Biomass (Mg ha ⁻¹)	65 (n=51)	38 (ref. 33)	2
Mosses	Ground cover (%)	55 (n=92)	4 ^b (ref. 34)	14
Biocrusts	Ground cover (%)	30 (n=140)	9 (ref. 35)	3

^aValues are mean abundances of N fixers or N-fixing substrates. For example, N-fixing trees comprised 79% of tree basal area across the studies in our database that reported tree BNF rates, compared with 3% of tree basal area globally. The ratio shows that BNF studies oversample N fixers 2–30 times (mean of 17 times) more than their abundance in natural ecosystems globally, suggesting sampling bias. The abundance data available for epiphytic lichens were qualitative and did not allow similar calculations. Sampling bias is not expected for soil and litter. See details in the Methods and Supplementary Information. *n* indicates the sample size. ^b<http://nfi.nfis.org>; www.polardata.ca; and www.slu.se/foreststatistics.

independent estimates of N fixer abundance, we quantify this sampling bias (Table 1) and show that field studies of BNF occur in geographical hotspots containing 26–30 times as many root-nodulating N-fixing trees, shrubs and herbs, 14 times as many N-fixing ground mosses and two to three times as much biocrust and dead wood as their mean abundances worldwide. Accounting for N fixer abundance in field BNF studies and globally would improve the estimates of natural terrestrial BNF. Global estimates of BNF are considerably more constrained for agricultural than natural terrestrial ecosystems²⁰. This is partly because data on land use area and production for the major N-fixing crops are readily available from the Food and Agriculture Organization^{20,21}. Previous global estimates of BNF by N-fixing crops as well as legumes in pastures that are intensively managed for forage and livestock production (cultivated pastures) (hereafter, we collectively refer to BNF in crops and cultivated pastures as ‘agricultural BNF’) increased from 32 Tg N yr⁻¹ to 70 Tg N yr⁻¹ over the past three decades, reflecting a marked increase in harvested area and production during the same period^{20,22–24}. Increased cultivation of N-fixing crops and forage has both enhanced food production and helped reduce reliance on synthetic N fertilizers²⁵. However, inefficiencies in the food production–consumption chain, including

food waste and insufficient N recycling, contribute to substantial losses of all forms of agricultural N, including BNF-derived N (ref. 24). This excess agricultural N cascades through terrestrial and aquatic ecosystems and the atmosphere, contributing to eutrophication, loss of biodiversity, reduced air and drinking water quality, and increased emissions of the greenhouse gas nitrous oxide²⁶. Proposed global and regional safe operating limits for agricultural N inputs are partly based on estimates of agricultural BNF^{7,8}. However, it is still uncertain how much N is fixed in cultivated pastures globally because of uncertainties in land use area, production and legume abundance in these systems²⁰. This uncertainty limits our understanding of the magnitude of agricultural BNF as a source of excess N globally. Here, we quantify the global distribution and magnitude of terrestrial BNF in all major N-fixing niches across natural and agricultural biomes. Our approach improves markedly on previous estimates in several ways. First, we extensively update the literature synthesis of BNF rates. Specifically, for natural biomes, our dataset includes 1,177 field BNF measurements (Fig. 1). This comprises 1,122 BNF rates (kg N ha⁻¹ yr⁻¹) for N-fixing prokaryotes²⁷ in symbiosis with root-nodulating trees, shrubs and herbs (hereafter ‘symbiotic niches’) and in soil, litter, dead wood, ground mosses, biocrusts and epiphytic lichens (hereafter ‘free-living niches’; although the group includes niches that fix N via symbiosis or association, that is, lichens, mosses and biocrusts) and 55 estimates of the percentage of N derived from the atmosphere (%N_{dfo}) for N-fixing herbs (that is, legume forbs)¹⁹. Previous global syntheses in refs. 3, 4 included around 100–250 BNF rates. Thus, we are more than quadrupling rate data on these critical BNF pathways that inform our estimates. Second, we synthesize data presented in BNF studies on the abundance of N fixers or N-fixing substrates (that is, the material in which N fixation occurs, for example, dead wood)¹⁹ and also assemble independent datasets that quantify N fixer and N-fixing substrate abundances in terrestrial biomes worldwide to resolve the main source of uncertainty and bias in past estimates of terrestrial BNF (Table 1). Third, we also update comprehensive BNF datasets for legume crops and forage from previous syntheses^{20,21,28,29} and compile BNF rates for non-legume N-fixing crops (rice and sugarcane). Finally, using these BNF datasets, we derive niche-specific estimates of BNF activity per unit of N fixer or N-fixing substrate abundance (Extended Data Tables 1 and 2). We then combine the estimates of BNF per unit of abundance with independent, spatially explicit data of the abundance of N fixers or N-fixing substrates from global or regional datasets for trees³⁰, shrubs³¹, herbs^{31,32}, dead wood³³, ground mosses³⁴ (<http://nfi.nfis.org>; www.polardata.ca; and www.slu.se/foreststatistics), biocrusts³⁵ and epiphytic lichens³⁶ in natural ecosystems, and legume crops³⁷ and forage legumes^{32,37} in agricultural

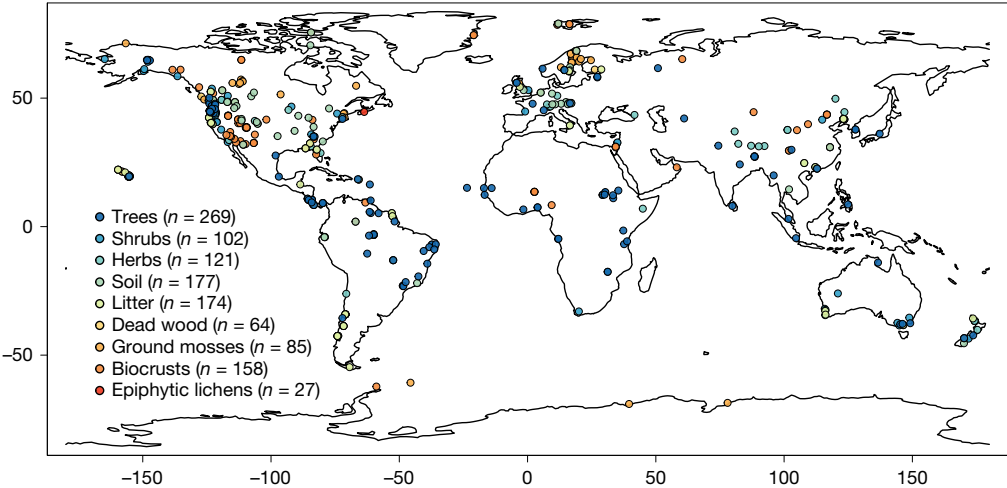


Fig. 1 | Location of field measurements of BNF in natural terrestrial biomes. Each point represents one BNF rate (kg N ha⁻¹ yr⁻¹) and/or percentage of nitrogen derived from the atmosphere (%N_{dfo}) value (n = 1,177). Not all points are visible because of overlap.

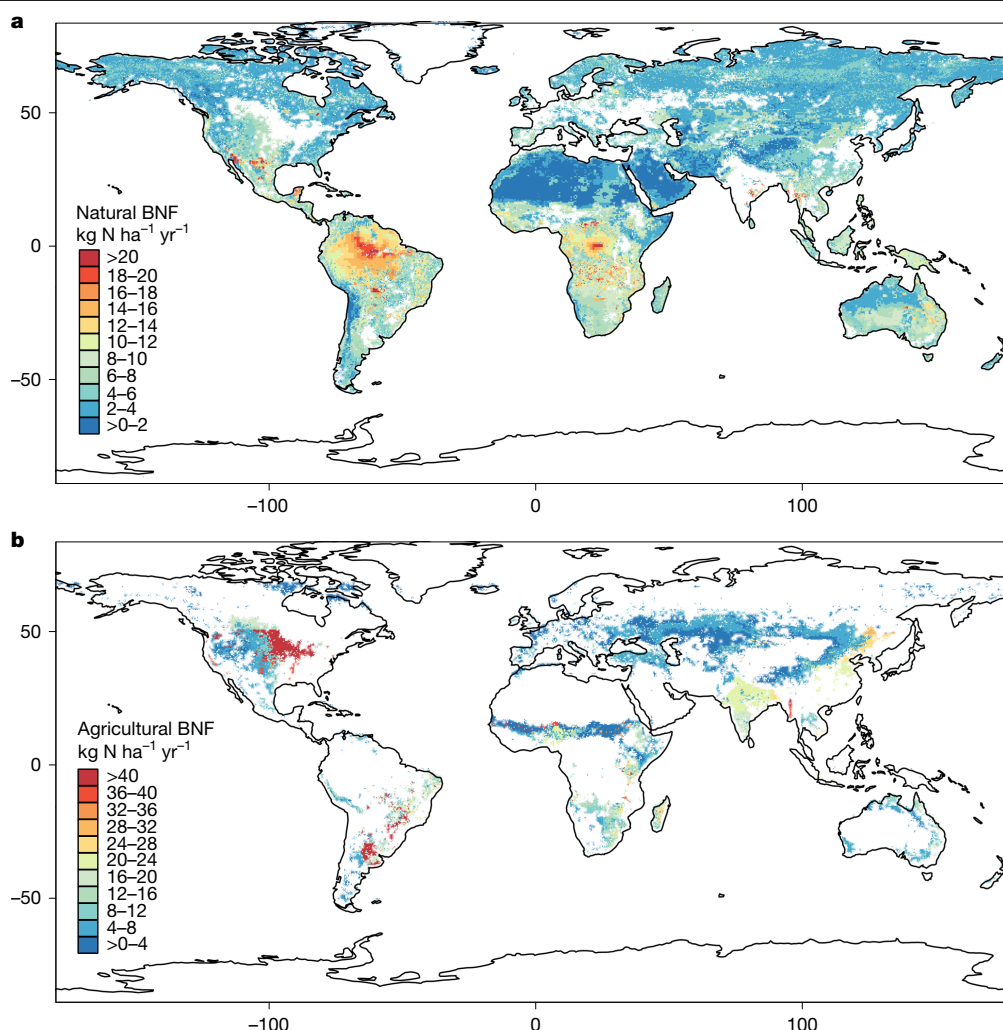


Fig. 2 | Global distribution of terrestrial BNF. a, b, Total mean BNF rates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) across natural (a) and agricultural (b) lands. Note the different colour scales for a compared with b. Natural BNF (a) combines all major natural N-fixing niches (root-nodulating N-fixing trees, shrubs and herbs; free-living BNF in soil, litter and dead wood; and BNF associated with ground mosses, biocrusts and epiphytic lichens) mapped across terrestrial lands, minus croplands. Agricultural BNF (b) combines N-fixing crops mapped across the

total land area of croplands (by country) and N-fixing forage mapped across the total land area of grasslands between 67°N/S (thus overlapping with natural grasslands in a), with rates adjusted to total land areas (see details in the Methods and Supplementary Information). Areas shown in white in both a and b comprise urban areas, areas with permanent snow and ice cover, and water bodies. Maps of CIs are in Extended Data Figs. 1 and 2.

ecosystems (Supplementary Table 1). With these combined data, we map the global distribution and estimate biome and global totals of BNF for each niche.

BNF in natural terrestrial biomes

We find that natural terrestrial biomes fix $65 (52-77) \text{ Tg N yr}^{-1}$ (mean and 68% confidence interval (CI), which is analogous to ± 1 standard error) (Fig. 2a, Extended Data Fig. 1 and Extended Data Tables 3 and 4). Our estimates are lower than previous bottom-up global syntheses based on field measurements of natural terrestrial BNF (Fig. 3a). The first comprehensive synthesis of natural terrestrial BNF was provided in ref. 3, reporting mean BNF inputs of 195 Tg N yr^{-1} with a range of $100-290 \text{ Tg N yr}^{-1}$. The primary driver of the more moderate global rates we report here is the lower abundance of N fixers in our estimates. In ref. 3, symbiotic N fixer coverages were assumed (based on limited data from BNF rate studies) to be 5–25% globally, whereas our estimates based on independent global and regional abundance data indicate only 2–3% coverage for symbiotic niches and 4–9% coverage for ground mosses and biocrusts (Extended Data Table 5).

To illustrate the importance of N fixer abundance to global BNF inputs, we performed additional calculations applying the assumed N fixer abundances reported in ref. 3 to the BNF dataset used here. These calculations resulted in BNF inputs of $140 (102-178) \text{ Tg N yr}^{-1}$ (mean and 68% CI) (Extended Data Tables 6 and 7), which are nearly double our primary estimates. This discrepancy underscores that much of the difference between our primary estimates and those of ref. 3 stems from our use of newly derived estimates of N fixer abundances. In a more recent effort⁴, natural terrestrial BNF was upscaled using only the subset of BNF rate studies that accounted for the abundance of N fixers in the landscape (without reporting how representative these studies were) and reported median BNF inputs of 88 Tg N yr^{-1} with an interquartile range of $52-130 \text{ Tg N yr}^{-1}$. Our central estimate of 65 Tg N yr^{-1} is 1/4 to 2/3 lower than these previous bottom-up central estimates, suggesting that markedly less new N than indicated in earlier estimates is available to support plant N demand, NPP and C storage in natural ecosystems worldwide.

Most terrestrial biosphere and Earth system models that link N to the global C cycle rely on global estimates of BNF, not only as benchmark data but also to inform how to model BNF^{5,6}. Many global models

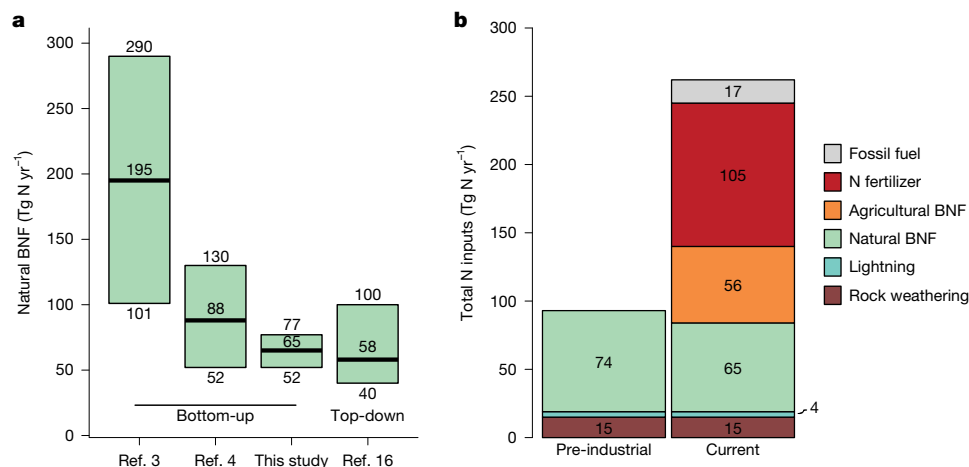


Fig. 3 | Global estimates of terrestrial N inputs to the land surface. a, b, Total natural BNF inputs (Tg N yr^{-1}) based on bottom-up and top-down scaling approaches (**a**) are shown along with central estimates of total N inputs (Tg N yr^{-1}) at pre-industrial and current times (**b**). The data in **a** show central and uncertainty estimates (68% CI) from this study and central and uncertainty or dispersion

simulate terrestrial BNF as a function of actual evapotranspiration (AET) or NPP^{5,6} based on empirical relationships for natural terrestrial biomes from ref. 3. The phenomenological relationship between BNF, AET and NPP in ref. 3 is consistent with conceptual and empirical evidence showing correlations among BNF rates, temperature, water and C availability, and plant N demand^{3,38}. As in ref. 3, we find positive biome-scale relationships between total natural BNF and both AET and NPP (Fig. 4a,b). We also find positive relationships between total natural BNF and both AET and NPP across 500 m grid cells (Fig. 4c,d), indicating that these relationships hold at multiple spatial scales. Overall, our BNF regressions deviate from observed values by an average of about $2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Supplementary Table 2). Using AET as a predictor of BNF results in total natural BNF inputs that are similar to our bottom-up estimates in most evaluations (Supplementary Table 2). Using NPP or AET and NPP together underestimates total natural BNF inputs by an average of about 9 Tg N yr^{-1} (Supplementary Table 2). Importantly, the slopes of the AET–BNF and NPP–BNF relationships in our updated dataset are about half those reported in ref. 3. This suggests that models using the equations from ref. 3 overestimate natural terrestrial BNF, particularly in warm, wet, highly productive regions, which are important areas of global terrestrial C uptake.

Our results point to evergreen broadleaf forests as global hotspots of natural terrestrial BNF, accounting for 76% of the total BNF in forest biomes (Fig. 5a). High BNF in evergreen broadleaf forests results from relatively large land areas dominated by tropical forests and two to four times higher BNF rates per area than other forest biomes (Fig. 5b). Within the evergreen broadleaf forest biome, tree symbioses are the largest single source of BNF (43%), with additional substantial inputs from soils and dead wood (20% and 18%, respectively). BNF per unit of N-fixing tree abundance is similar across forest biomes (Extended Data Table 1). Thus, high rates of symbiotic N fixation by trees in evergreen broadleaf forests reflect higher N-fixing tree abundance in this biome (2–60 times higher than other forest biomes; Extended Data Table 5). High BNF inputs by dead wood in evergreen broadleaf forests result from both large stocks of dead wood in the tropics³³ (Extended Data Table 5) and relatively high BNF per unit of dead wood mass (Extended Data Table 1). Savannas and grasslands together account for half (51%) of total natural BNF inputs worldwide, highlighting large BNF inputs in non-forest biomes (Fig. 5a). Soils and root-nodulating herbs are the largest BNF sources in savannas and grasslands (about 35% and 27%, respectively, in both biomes), and biocrusts are also important in grasslands (33%). High total BNF inputs in savannas and grasslands are

estimates (high and low estimates or interquartile range) from previous syntheses. The data in **b** are from ref. 1 for rock weathering, ref. 46 for N fixation by lightning, ref. 37 for synthetic N fertilizer use, ref. 24 for fossil fuel emissions and this study for natural and agricultural BNF.

partly because of their extensive land areas and relatively high abundances of root-nodulating N-fixing herbs (Extended Data Table 5). High biocrust BNF inputs in grasslands reflect a combination of relatively high BNF rates per unit of biocrust cover (Extended Data Table 1) and high biocrust coverage (Extended Data Table 5). Overall, our results showing high BNF rates and N fixer abundances in tropical forests and drylands are consistent with the views that N limitation may occur at low latitudes in addition to high latitudes^{11,39,40} and that BNF is an important source of new N needed to sustain global terrestrial productivity^{11,13}.

Globally, the niches that represent the largest sources of natural terrestrial BNF are non-agricultural soils (26%), followed by root-nodulating N-fixing trees (19%), biocrusts (18%) and root-nodulating N-fixing herbs (17%) and shrubs (9%) (Extended Data Table 4). Symbiotic niches can provide substantial BNF inputs per area and more directly affect terrestrial NPP via N fixer biomass accumulation, but their presence in natural ecosystems is patchy. By contrast, free-living niches provide relatively lower BNF inputs per area and indirectly affect terrestrial NPP by enriching ecosystems with N but are more evenly distributed across the surface of Earth^{41,42}. Together, all free-living niches account for 56% (53–58%) of total BNF inputs in natural biomes, with the greatest contributions from soils and biocrusts (Extended Data Table 4). Large BNF inputs in non-agricultural soils reflect the vast amount of soil and its relatively high BNF rates per area (Extended Data Table 3), even though reliable estimates are limited to the top 10 cm of soil because of insufficient field data from subsoil¹⁹. Our estimates of global BNF inputs from biocrusts (mean of 12; 68% CI of 9–14 Tg N yr^{-1}) are at the lower end of estimates from previous efforts (for example, mean of 24; range of 3–46 Tg N yr^{-1}) (refs. 35,43), because of lower biocrust BNF rates and coverage in our updated datasets, yet biocrusts nevertheless remain a notable global source of BNF. The widespread and quantitatively important role of free-living BNF underscores the importance of including both symbiotic and free-living BNF pathways in terrestrial biosphere and Earth system models. More robust data on symbiotic and free-living BNF are particularly important for constraining models that differentiate between these BNF pathways^{44,45}.

Terrestrial BNF modified by agriculture

We find that N-fixing crops and legumes in cultivated pastures fix 56 (54–58) Tg N yr^{-1} (mean and 68% CI) (Fig. 2b, Extended Data Fig. 2 and Extended Data Tables 3 and 4). Legume crops fix 33 (33–34) Tg N yr^{-1} , representing 60% of total agricultural BNF (Fig. 5a). Our BNF estimates

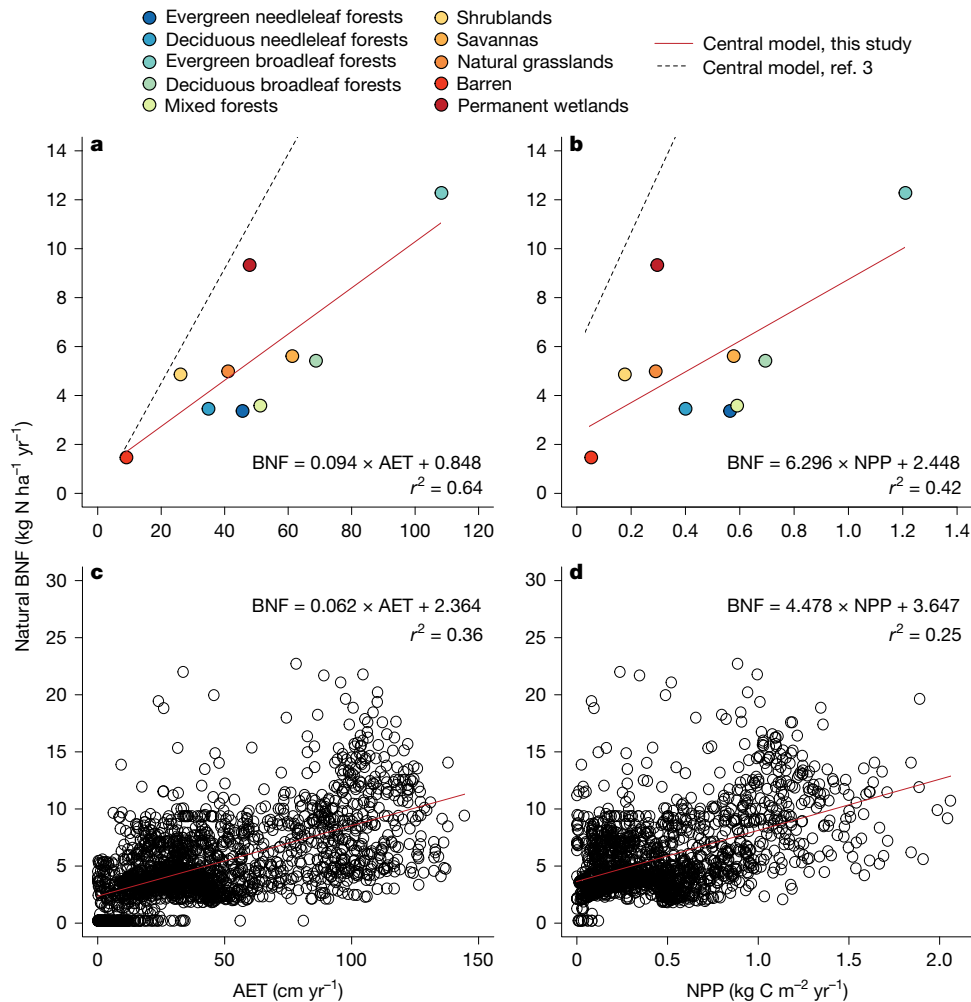


Fig. 4 | Relationships of global natural terrestrial BNF with AET and NPP. **a–d**, Central estimates of natural BNF rates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) from Fig. 2a are shown as functions of AET (**a,c**) and NPP (**b,d**) using biome means (**a,b**) and a sample of 10,000 grid cell values at regular intervals (**c,d**). The central models from ref. 3 are plotted as black dotted lines on **a** and **b** for comparison. The models from

ref. 3 are based on similar ranges of AET and NPP as the symbols on **a** and **b**, but project BNF rates beyond the values presented here. Relationships using AET and NPP together as drivers and with the intercept forced through zero are in Supplementary Table 2. See details and notes on the use of these relationships in the Methods. The source data for **a** and **b** are in Supplementary Table 3.

for legume crops, which are derived from 2019 data, are similar to the global value of 36 Tg N yr^{-1} reported for 2018 (ref. 20) but 50% higher than 22 Tg N yr^{-1} reported for 2005 using similar methodologies based on grain production data²³. Legumes in cultivated pastures are the second largest source of BNF in agriculture, fixing $20 (19\text{--}20) \text{ Tg N yr}^{-1}$ (35% of the total), followed distantly by N fixation associated with rice paddies and sugarcane (5% of the total) (Fig. 5a and Extended Data Table 4). Our estimates for legume-based BNF in cultivated pastures are within the range of previous estimates based on BNF rates per area, $12\text{--}30 \text{ Tg N yr}^{-1}$ (refs. 20,23). Our agricultural BNF estimates are higher than the estimates of 32 Tg N yr^{-1} and 40 Tg N yr^{-1} based on BNF rates per area reported for the years 1995 and 2005, respectively^{22,24}. Our values are, however, within the lower end of agricultural BNF estimates based on legume grain production and forage BNF rates per area, 50 Tg N yr^{-1} and 70 Tg N yr^{-1} , reported for the years 2005 and 2018 (refs. 20,23), largely owing to our more moderate estimates for cultivated pastures. Despite methodological differences between the current and previous estimates, our results indicate that agricultural BNF has risen by 75% during the past two decades, largely driven by the 94% increase in harvested area of soybeans and the accompanying 165% increase in soybean production³⁷.

Estimates of pre-industrial terrestrial BNF (that is, before the global N cycle was transformed by human activities) offer quantitative evidence

of how land use and cover change and cultivated BNF have affected terrestrial BNF inputs. In a pre-industrial scenario, in which we assign all land area to natural biomes and use our natural biome BNF rates, terrestrial BNF would be $74 (59\text{--}89) \text{ Tg N yr}^{-1}$ (mean and 68% CI) (Extended Data Table 8). This value is higher than the central estimate, yet within the range of a unique top-down pre-industrial estimate of global natural terrestrial BNF (58 Tg N yr^{-1} ; range $40\text{--}100 \text{ Tg N yr}^{-1}$) based on isotopic constraints on the global N budget¹⁶. The convergence between this top-down value and the progressive decline in bottom-up estimates (Fig. 3a) suggests increasing certainty in natural terrestrial BNF estimates. However, the top-down approach did not account for the spatial distribution of BNF among the biomes of Earth. Before modern agriculture, BNF represented the largest source of N inputs to the land surface (74 Tg N yr^{-1}), followed by rock weathering (15 Tg N yr^{-1}) (ref. 1) and lightning (4 Tg N yr^{-1}) (ref. 46) (Fig. 3b). The conversion of natural land to agriculture has, however, reduced natural terrestrial BNF globally by 12% compared with pre-industrial times, particularly in forests and shrublands (Extended Data Table 8). This conversion has also markedly increased the relative contribution of symbiotic BNF (including agricultural BNF) to 68% (65–72%) globally by favouring agriculturally important legumes (Fig. 5a). Agriculture has increased global terrestrial BNF from $74 (59\text{--}89) \text{ Tg N yr}^{-1}$ (before agricultural land use; Extended Data Table 8) to $120 (106\text{--}136) \text{ Tg N yr}^{-1}$, the current

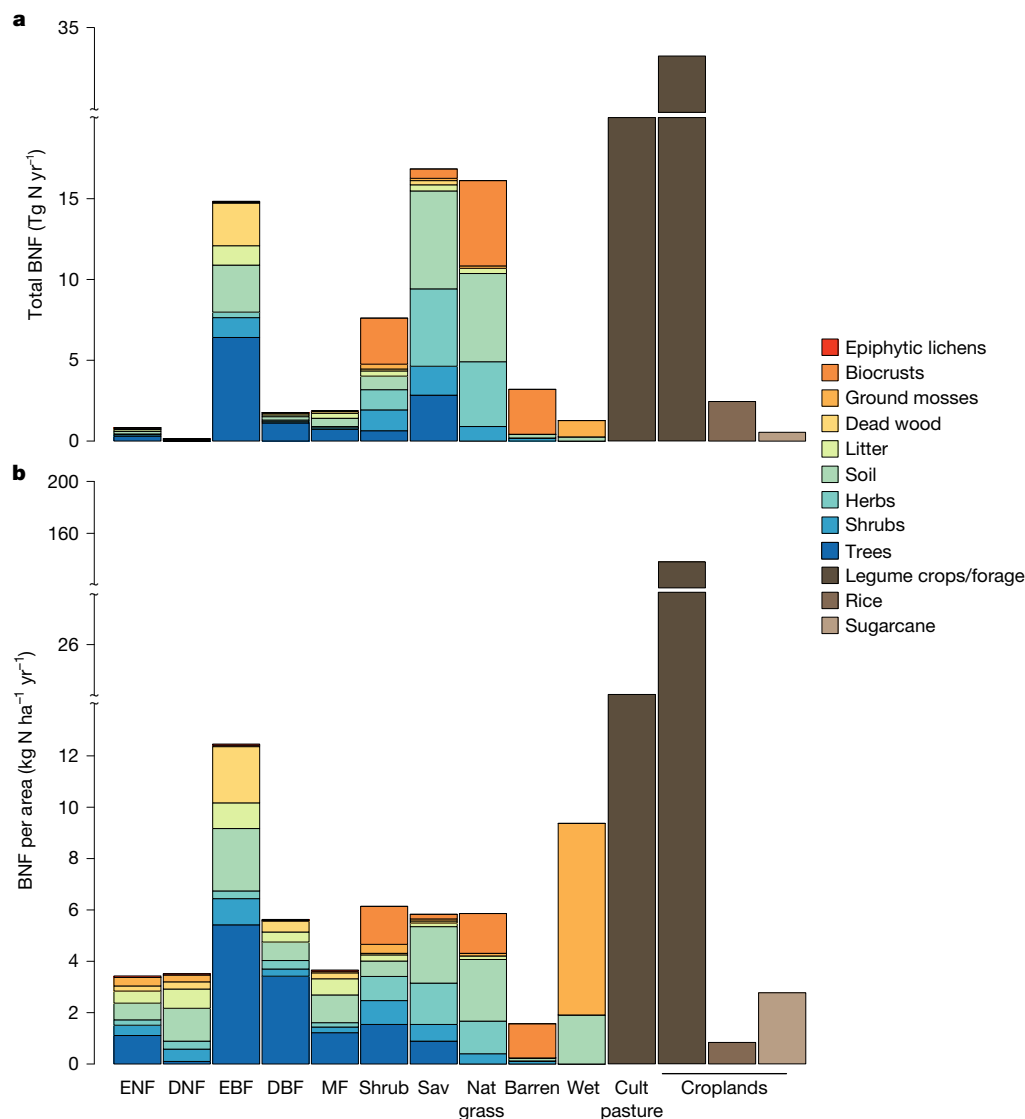


Fig. 5 | Biome and niche contribution to global terrestrial BNF. a,b, Total BNF inputs (Tg N yr^{-1}) (a) and BNF rates per area ($\text{kg N ha}^{-1} \text{yr}^{-1}$) (b) in natural and agricultural biomes. ENF, evergreen needleleaf forests; DNF, deciduous needleleaf forests; EBF, evergreen broadleaf forests; DBF, deciduous broadleaf

forests; MF, mixed forests; Shrub, shrublands; Sav, savannas; Nat grass, natural grasslands; Wet, permanent wetlands; Cult pasture, cultivated pastures. Note the broken y-axes. The source data are in Extended Data Tables 3 and 4.

total across both natural and agricultural lands (Extended Data Table 4). Thus, the global modification of terrestrial BNF by agriculture represents a 64% (53–80%) increase relative to pre-industrial rates.

Placing our results in a broader context, we find that agricultural BNF has altered the global N cycle more than previously recognized^{22,24,47}. Specifically, agricultural BNF has increased total terrestrial N inputs by 60% over pre-industrial levels (Fig. 3b). This places agricultural BNF as the second largest anthropogenic alteration to terrestrial N inputs, after inputs of synthetic N fertilizers and ahead of fossil fuel emissions, which have raised total terrestrial N inputs by 113% and 18% relative to pre-industrial rates, respectively. Overall, human activity has increased global terrestrial N inputs by about 180% from pre-industrial levels (Fig. 3b). Much of the global increase in N inputs helps feed humanity, but it also releases excess N to the environment with effects ranging from aquatic eutrophication to greenhouse warming to reduced biodiversity^{24,26}. Our results help focus on opportunities for achieving a safe operating space for global N cycling^{7,8}. The high rates of agricultural BNF and N fertilizer use, combined with our down-revised estimate of natural BNF, reinforce that the main sources of excess N worldwide occur along the food production–consumption chain. Current N inputs from

agricultural BNF alone (56 Tg N yr^{-1}) are approaching planetary boundaries for safe global N cycling^{7,8}, and similar to N fertilizer inputs, can be managed to sustain humanity and minimize environmental harm.

Conclusions

By using data on N fixer abundances to generate a new global estimate of terrestrial BNF flux, we find lower natural BNF inputs than are typically considered in analyses of the global N cycle^{1,13,14,22,24}, which has important implications for understanding and simulating the terrestrial N cycle. Foremost, our results reinforce a central idea in biogeochemistry that low rates of BNF contribute to widespread N limitation of NPP^{11,12,16}. Lower BNF inputs further imply that more modest rates of ecosystem N loss are sufficient to maintain long-term N balances³⁸ and act as an additional constraint on global-scale estimates of hydrologic and gaseous N fluxes in the biosphere¹⁶. Finally, our findings indicate that BNF can impose stronger constraints on terrestrial C storage than previously thought^{13,14}.

Our updated and spatially explicit estimates of BNF in both natural and agricultural ecosystems can improve assessments of critical

ecosystem services related to the provision of clean air and water, C sequestration, and the maintenance of agricultural productivity at regional to global scales. For instance, although recent terrestrial biosphere and Earth system models yield similar total terrestrial BNF estimates of 106–140 Tg N yr⁻¹ (refs. 5,6), the apportionment of BNF sources in these models is markedly different from our results. Most of these models apply BNF functions from ref. 3 to all land areas, which overestimates BNF in natural biomes and underestimates BNF across agricultural lands. Our empirical analysis indicates about 67% lower BNF inputs across natural lands than ref. 3, and that nearly 50% of total terrestrial BNF fluxes occur in agricultural lands, although N-fixing crops and forage cover only 6% of the total global land area, highlighting the substantial modification of global terrestrial BNF by human activities.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-025-09201-w>.

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Methods

BNF dataset in natural biomes

A detailed description of the BNF dataset in natural terrestrial biomes, including the literature search, inclusion criteria and dataset structure, is provided in ref. 19. Briefly, it comprises studies carried out in the field or other settings simulating field conditions in unmanaged and managed ecosystems (for example, silviculture/forestry, rangelands and agroforestry systems) but not in grain croplands or cultivated pastures. It includes a total of 1,207 BNF rates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) for symbiotic (trees, shrubs and herbs) and free-living niches (soil, litter, dead wood, mosses, lichens and biocrusts) from 328 studies. Here we used a subset of the BNF rates in the original dataset ($n = 1,122$) that matched our upscaling approaches, as detailed below. All BNF rates were based on well-established methods, including acetylene reduction assay, $^{15}\text{N}_2$ incorporation, ^{15}N natural abundance, ^{15}N dilution, N accretion, N accumulation and mass balance of other N fluxes. The BNF rates were originally reported in either $\text{kg N ha}^{-1} \text{yr}^{-1}$ or similar units (for example, $\text{g N m}^{-2} \text{yr}^{-1}$) or were converted to these units from cumulative or sub-annual BNF or ARA rates per unit of area or N fixer abundance, or the percentage of N derived from the atmosphere ($\%N_{\text{dfa}}$). These rate conversions are described in detail in ref. 19. All converted BNF rates fell within the range of values originally reported in the literature in $\text{kg N ha}^{-1} \text{yr}^{-1}$ units¹⁹. The BNF rates show a right-skewed frequency distribution for each niche¹⁹, indicating frequent low and infrequent high values, typical of BNF fluxes in natural ecosystems^{48,49}. The dataset also includes 152 estimates of herb $\%N_{\text{dfa}}$ based on ^{15}N natural abundance or ^{15}N dilution methods. We used a subset of herb $\%N_{\text{dfa}}$ values ($n = 55$), as detailed below. Most BNF rates and $\%N_{\text{dfa}}$ values were measured between the years 2000 and 2020 (59%)¹⁹. The location of study sites in the dataset spans the global range of temperature and precipitation (average of 2000–2020 from ref. 50), suggesting the dataset is representative of the heterogeneity of environmental conditions that drive BNF rates¹⁹. The dataset also contains data on N fixer relative basal area and relative density for trees, N fixer percentage ground cover for shrubs, herbs, mosses and biocrusts, and dead wood biomass in the BNF studies (Table 1). Published estimates of BNF rates, $\%N_{\text{dfa}}$ or N fixer abundance from plots and stands that differ in vegetation composition or dominance, age, disturbance history, N fixer abundance, elevation/climate and/or topographic setting within the same study area constitute independent entries in the dataset.

The dataset also provides the International Geosphere-Biosphere Program (IGBP) land cover class⁵¹ associated with each data entry (Supplementary Table 4). It does not distinguish, however, between the land cover classes ‘Closed Shrublands’ and ‘Open Shrublands’ or between the classes ‘Woody Savannas’ and ‘Savannas’ because most BNF studies lacked the necessary information for these finer classifications. Data entries in these systems were classified as ‘Shrublands’ and ‘Savannas’.

We used a subset of the BNF rates ($n = 1,122$) and $\%N_{\text{dfa}}$ values ($n = 55$) in the original dataset that matched our upscaling approaches (Fig. 1). For trees, shrubs, dead wood, ground mosses and biocrusts, we used only BNF rates with paired N fixer or N-fixing substrate abundance data. For soil, litter and epiphytic lichens, we used all BNF rates available. To explore the implications of using an alternative upscaling approach based on methods applied in ref. 3, we also used the full set of BNF rates originally reported in $\text{kg N ha}^{-1} \text{yr}^{-1}$ or similar units for all niches, regardless of whether corresponding abundance data existed. In both approaches, we used community-level rates or $\%N_{\text{dfa}}$ for studies with more than one N-fixing species. See Supplementary Information for further details.

BNF dataset in croplands

The BNF dataset for legume crops includes 5,374 field-based $\%N_{\text{dfa}}$ observations for soybean, groundnut and pulses (common bean, green gram, black gram, chickpea, cowpea, field pea, pigeon pea, lentil, broad

bean, lupin, vetches and Bambara groundnut) from 329 reports²¹. The $\%N_{\text{dfa}}$ estimates were obtained using ^{15}N natural abundance, ^{15}N dilution and N accumulation methods under N fertilization levels typically used by farmers. A second dataset contains more than 4,000 observations of coefficients required for upscaling grain legume $\%N_{\text{dfa}}$ (harvest index, shoot N concentration and belowground factor) from 224 reports²⁰. Detailed descriptions of these datasets are provided in refs. 20,21.

We also accounted for BNF by non-legume crops for which sufficient BNF data are available: rice and sugarcane. We compiled BNF rates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) by *Azolla*–cyanobacteria associations and free-living cyanobacteria in soils of rice systems under N fertilization. We found six studies that matched these criteria (Supplementary Table 5). The BNF rates were estimated using ^{15}N dilution, $^{15}\text{N}_2$ incorporation and mass balance methods under N fertilization rates ranging from 30 kg N ha^{-1} to 250 kg N ha^{-1} . Evidence of substantial and consistent BNF in sugarcane systems is definitive for Brazil, but not for other countries^{23,52}. We used endophytic/associative BNF rates in sugarcane systems in Brazil, estimated using the ^{15}N natural abundance method in ref. 53 (Supplementary Table 6), to upscale sugarcane BNF for Brazil alone. The rates in ref. 53 were based on $\%N_{\text{dfa}}$ values estimated under no N fertilization but within the range of $\%N_{\text{dfa}}$ values estimated under N fertilization levels typically applied in sugarcane systems in Brazil (40 – 80 kg N ha^{-1}) (refs. 53,54). It is worth noting that the average rate of N fertilizer applied to sugarcane in Brazil of 76 kg N ha^{-1} is substantially less than the rates of 444 kg N ha^{-1} and 184 kg N ha^{-1} for the other major producers, China and India, respectively⁵⁵.

We did not account for other sources of BNF in croplands, such as free-living BNF in soils or endophytic/associative BNF beyond that of sugarcane in Brazil, because field data are scant, and most of those that exist are marked by methodological constraints that prevent distinguishing N inputs via BNF compared with N deposition²³. Moreover, given that soils in natural ecosystems sustain BNF rates of 1 – $2 \text{ kg N ha}^{-1} \text{yr}^{-1}$ in the absence of N fertilizer (Extended Data Table 1) and that soil BNF is suppressed by N additions⁵⁶, we assume that BNF would be markedly suppressed in cropland soils receiving N fertilizer. An exception is rice paddies, in which cyanobacteria sustain BNF rates of 3 – $4 \text{ kg N ha}^{-1} \text{yr}^{-1}$ under N fertilization⁵⁷.

BNF dataset in cultivated pastures

The BNF dataset in cultivated pastures comprises a total of 168 observations of aboveground BNF rates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) and aboveground dry matter production ($\text{Mg ha}^{-1} \text{yr}^{-1}$) for perennial forage legumes in northern temperate and boreal areas from 36 studies²⁸. It includes data for *Trifolium pratense*, *T. repens*, *Medicago sativa* and other legumes planted in monocultures or mixtures with grasses under N fertilization rates ranging from 0 to more than 200 kg N ha^{-1} . The BNF rates were based on ^{15}N dilution, ^{15}N natural abundance and N accumulation methods. A detailed description of this dataset is provided in ref. 28. To our knowledge, a similar dataset is not available for tropical or southern temperate regions. Nevertheless, the BNF rates reported in ref. 28 are almost identical to those found for perennial legumes in sub-tropical and temperate pastures in the southern hemisphere⁵⁸. We assume that the relationship between BNF rates and productivity for forage legumes in northern boreal and temperate regions (Supplementary Information) also applies to other regions worldwide. We did not account for BNF in soils of cultivated pastures for the same reasons as explained above for croplands.

Abundance datasets

We prioritized using global gridded datasets for quantifying N fixer abundance. These were available for trees³⁰, herbs in natural biomes and cultivated pastures³² and biocrusts³⁵ (Supplementary Table 1). We used grid cell values of N fixer abundance in BNF upscaling raster calculations. When global gridded datasets were not available, we used abundance data from global or regional databases or inventories.

This was the case for shrubs³¹, dead wood³³, ground mosses³⁴ (<http://nfi.nfis.org>; www.polardata.ca; and www.slu.se/foreststatistics), epiphytic lichens³⁶ and N-fixing crops³⁷. For shrubs, dead wood, ground mosses and epiphytic lichens, we estimated IGBP biome-level means of N fixer or N-fixing substrate abundance for the global upscaling. For N-fixing crops, we used country-level production data³⁷. No abundance datasets were used for soil and litter because we do not expect sampling bias regarding substrate abundance for these niches. A detailed description of the abundance datasets and calculations is in Supplementary Information.

Global upscaling of BNF

Our approaches build on previous efforts to upscale field measurements of BNF using N fixer abundance for trees in the United States⁵⁹ and biocrusts³⁵ and legume crops^{20,21} globally. Using the BNF datasets described above, we derived estimates of BNF activity per unit of N fixer or N-fixing substrate abundance (Extended Data Tables 1 and 2). We summarized BNF activity per unit of N fixer or N-fixing substrate abundance in IGBP biomes, in which the niche was present in the spatial abundance datasets (Supplementary Information). Unless otherwise indicated, to substitute BNF activity in natural biomes with a limited number of estimates ($n < 3$), we used the mean in forest biomes and the mean in open biomes (shrublands, savannas, grasslands and barren) to substitute BNF activity in forest and open biomes, respectively. We combined our IGBP biome-specific estimates of BNF activity per unit of abundance of N fixers or N-fixing substrates with spatial abundance data of N fixers or N-fixing substrates (Supplementary Table 1) and IGBP land cover data in 2019 (ref. 51) (Supplementary Table 4) to create BNF rate ($\text{kg N ha}^{-1} \text{yr}^{-1}$) global gridded datasets for each niche (Supplementary Information). We also created total natural terrestrial and total agricultural global gridded BNF rate datasets and maps (Fig. 2 and Extended Data Figs. 1 and 2).

Accounting for agricultural BNF in this framework required adjustments to address the lack of available land cover data of N-fixing crops and forage. We assigned crop- and country-specific BNF rates to IGBP cropland areas by country and mapped crop BNF across the total land area of IGBP croplands. We adjusted crop BNF rates per area in gridded datasets and maps to account for the proportional cover of N-fixing crops per grid cell. We split the land area of IGBP grasslands into natural grasslands and cultivated pastures based on the estimate that cultivated pastures covered 26% of global grasslands in 2019 (ref. 37). Specifically, we assigned 27% of the area of each grid cell between 67° N/S (ref. 28) as cultivated, and the rest as natural. We then applied N fixation rates for natural grasslands and N-fixing forages, respectively. This results in an overlap of the mapped spatial cover of natural grasslands and cultivated pastures. To correct this overlap, we adjusted BNF rates per area by both N-fixing forages and all niches in natural grasslands downwards to account for their proportional cover per grid cell. We note that N-fixing crops and forage have more limited distribution globally and sustain higher BNF rates per area in the fields of farmers (Extended Data Table 3) than indicated in our gridded datasets and maps. Although gridded land use data would have improved the spatial distribution of our agricultural BNF estimates, it would not have affected our totals (Extended Data Table 4).

As in previous global BNF syntheses^{3,4,20,21}, we accounted for all main BNF niches for which extensive data were available. However, our estimates do not account for all possible BNF sources. There are free-living niches in both natural and agricultural systems, for example, plant endophytes and epiphylls, rhizosphere and BNF by insects such as termites and ants, for which BNF data are too limited to generate robust global estimates⁴². Summaries of BNF rates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) weighted by land area and BNF inputs (Tg N yr^{-1}) by niche by biome and global totals are in Extended Data Tables 3 and 4. In these and all other tables, 'Not determined' (ND) indicates cases in which estimating BNF was not appropriate. For natural biomes, ND indicates biomes in which

the niche was not present in the spatial abundance datasets. ND also applies to niches that were present in permanent wetlands, but for which BNF data were absent or very limited (shrubs, herbs and litter), and substituting data from other biomes was not appropriate. For agricultural biomes, ND applies to niches not present or not considered important sources of BNF (for example, soils in legume crop and forage systems, as explained above). Further discussion on knowledge gaps and priorities for future global BNF syntheses is provided in the Supplementary Information.

Alternative upscaling approaches

As a secondary approach, we estimated natural terrestrial BNF using similar methods as in ref. 3 to evaluate the leverage of different N fixer abundances on global estimates. For this, we used the subset of BNF rates originally reported in $\text{kg N ha}^{-1} \text{yr}^{-1}$ or similar units¹⁹. First, we summarized BNF rates by niche by biome and filled data gaps to account for niche spatial coverage as described for the main upscaling approaches. Next, we adjusted BNF rates by trees, shrubs and herbs to an assumed N fixer cover of 15%, the overall mid-range value used in ref. 3 (Extended Data Table 6). Then, we multiplied the biome BNF rates for each niche by the corresponding IGBP biome land cover area (ha) in the year 2019 (ref. 51) to estimate BNF inputs (Tg N yr^{-1}) by niche by biome and global totals (Extended Data Table 7).

We also estimated pre-industrial terrestrial BNF to quantify how land use and cover change and agricultural BNF have affected global terrestrial BNF and total terrestrial N inputs (Fig. 3b). We found no evidence of temporal trends in the natural BNF rates used here (data not shown). Therefore, we relied on our primary natural BNF estimates, which combined BNF activity with N fixer abundance data, to estimate pre-industrial BNF. However, we note that N fixer abundance^{60,61} and natural BNF rates^{62,63} might have changed with global environmental change since pre-industrial times. We summarized biome-level simple means of grid cell values of BNF rates ($\text{kg N ha}^{-1} \text{yr}^{-1}$) for each niche in natural biomes from our primary estimates. Then, we multiplied the biome-level mean BNF rates for each niche by the corresponding IGBP biome land cover area (ha) in the year 1500 CE in ref. 64 to estimate pre-industrial BNF inputs (Tg N yr^{-1}) by niche by biome and global totals (Extended Data Table 8). The IGBP land cover product in 1500 CE includes a small area of croplands (<1%) that we assigned to natural grasslands for this calculation. We compare our bottom-up pre-industrial estimate with a unique top-down pre-industrial estimate of global natural terrestrial BNF¹⁶. We note that N-fixing crops and forage were cultivated during pre-industrial times. A previous work²² reported agricultural BNF inputs of 15 Tg N yr^{-1} for the year 1860, which we hindcast for 1500 CE to 5 Tg N yr^{-1} based on differences in human population.

Relationships of BNF with AET and NPP

Many terrestrial biosphere and Earth system models represent terrestrial BNF as a function of AET or NPP^{5,6} based on empirical relationships for natural terrestrial biomes in ref. 3. We evaluated relationships of total natural terrestrial BNF ($\text{kg N ha}^{-1} \text{yr}^{-1}$) (Fig. 2a) as functions of AET and NPP and compared our relationships with those in ref. 3. We used the AET (cm yr^{-1}) global gridded product at 0.04° resolution (average of 2000–2020) from ref. 50. We resampled it to the same resolution as our BNF dataset (0.004°) using the bilinear method. For NPP, we used the MODIS NPP ($\text{kg C m}^{-2} \text{yr}^{-1}$) global gridded product at 0.004° resolution (average of 2001–2020) from ref. 65. To compare with ref. 3, which reported linear regressions using biome averages, we evaluated linear regressions at the biome scale using simple means of grid cell values (Fig. 4a,b and Supplementary Tables 2 and 3). We also evaluated linear regressions at the grid cell scale, using a sample of 10,000 individual grid cell values in regular intervals⁶⁶ to evaluate whether these relationships occur at multiple spatial scales (Fig. 4c,d and Supplementary Table 2). Linear regressions using all grid cell values at a

coarser 1° resolution gave similar results to our fine-scale resolution regressions (data not shown).

The use of one of the relationships reported here to predict natural terrestrial BNF depends partly on the spatial scale of interest (biome compared with grid cell). The biome-scale relationships do not account for land area coverage, so biomes with smaller distributions have the same weight as biomes with larger distributions. The opposite is true for grid cell-scale relationships, for which biomes with larger distribution (that is, more grid cells) have a greater weight than biomes with smaller distribution. Still, scaling global natural BNF using our biome-scale relationships results in values closer to our bottom-up estimates than scaling with grid cell-scale relationships (Supplementary Table 2). The relationships without the intercept forced through zero most accurately represent the data and estimate total natural BNF inputs closer to our bottom-up estimates (Supplementary Table 2) but probably overestimate BNF when AET and NPP are close to zero, particularly where biocrusts are not abundant, compared with relationships with the intercept forced through zero. Temporal trends have been reported for global terrestrial AET^{67,68} and NPP^{69,70} rates. Therefore, although the relationships reported here represent current natural BNF, AET and NPP, it is unclear whether they would also represent the relationships between these processes in the past or future.

Statistical analyses

A large proportion of BNF in natural ecosystems can happen in hotspots and during hot moments of activity (that is, geographic areas where and periods of time when BNF is active and relatively high compared with surrounding areas and time periods, respectively), so the arithmetic mean is a good descriptor of BNF rates in these systems as it is sensitive to these conditions⁷¹. But it is difficult to know whether extreme BNF values in the literature represent hotspots or hot moments of activity, or potential measurement or upscaling errors. Therefore, here we used the 2.5% trimmed mean (arithmetic mean after removing the 2.5% highest and 2.5% lowest BNF activity values in the dataset)⁷² for each niche to not overly represent extreme BNF values in our estimates of global natural BNF. For agricultural systems, we used the arithmetic means of BNF activity per unit of N fixer abundance updated from previous syntheses^{20,21}.

As in previous field-based bottom-up global BNF syntheses, the uncertainty inherent to each BNF measurement was not available and could not be accounted for in global estimates^{3,4}. Reference 3 recognized that N fixer abundance was the most important source of uncertainty in their estimates and upscaled BNF using low, central and high estimates of symbiotic N fixer abundance in BNF studies (without verifying its representativeness globally). Reference 4 used only BNF rate data that accounted for N fixer abundance in the landscape (also without verifying their representativeness globally) and reported inter-quartile range estimates of these BNF rates, which indicate the spread of the underlying data instead of uncertainty. Given that our goal was to provide global total estimates, we quantified the uncertainty in our estimates. Our abundance data were based on much larger and better-constrained datasets than our BNF rate data. Therefore, we focused on the uncertainty of BNF rate data. We used nonparametric bootstrapping with replacement to sample the niche datasets of BNF activity per unit of N fixer or N-fixing substrate abundance 1,000 times and estimated 68% CIs (analogous to ± 1 standard error; 95% CIs are analogous to ± 2 standard errors and approximately twice 68% CIs) (ref. 72) (Extended Data Tables 1 and 2), which we propagated through our calculations. We compared our results with the best estimates from previous syntheses, although these were estimated using different measurements of central tendency and uncertainty³ or dispersion⁴.

To report the uncertainty of our total natural terrestrial and total agricultural estimates, we propagated uncertainty per grid cell by converting niche BNF rate 68% CIs to standard error, propagating standard errors as the square root of the sum of the squares, then converting

them back to 68% CIs. We evaluated whether incorporating covariance in BNF rates among niches in natural biomes would affect total lower- and upper-bound estimates. To do that, we propagated niche mean standard errors by IGBP biome with and without covariance terms for each pair of niches. Lower- and upper-bound estimates were similar, either accounting for covariance among niches or not (data not shown), so we propagated uncertainty without covariance.

We evaluated relationships of natural BNF with AET and NPP using AET and NPP as predictor variables separately or together, with and without interaction, forcing the intercept to fit the data or through zero (Supplementary Table 2). We estimated the coefficient of determination (r^2), the root mean square error, the mean absolute error and the resulting global total natural BNF input (Tg N yr⁻¹) for each regression.

All analyses were performed in R v.4.3.0 (<https://www.R-project.org/>). We used the packages raster⁷³ and terra⁶⁶ for raster processing, calculations and analyses.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The global gridded datasets of BNF generated here are available in the ScienceBase repository (ref. 74) (<https://doi.org/10.5066/P13THKNR>). The underlying BNF rate dataset in natural terrestrial biomes is also available in ScienceBase (ref. 75) (<https://doi.org/10.5066/P1MFVBHK>). All other data are available from the databases cited or are in the main text or the Supplementary Information.

Code availability

All analyses were conducted using publicly available code packages: raster (ref. 73) and terra (ref. 66).

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Acknowledgements This paper is a contribution from a working group on BNF supported by the US Geological Survey (USGS) John Wesley Powell Center for Analysis and Synthesis (G19AC00036, S.S.P., D.N.L.M., C.C.C., S.C.R.). This research was supported in part by an

appointment to the USGS Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the US Departments of Energy (DOE) and Interior (DOI) under DOE contract no. DE-SC0014664. D.N.L.M. was funded by the National Science Foundation (IOS-2129542). S.A.B. was funded by the Leverhulme Trust and the Natural Environment Research Council (NE/S009663/1 and NE/M019497/1). J.P. was funded by the European Research Council under the European Union's Horizon 2020 Research and Innovation Programme (819202). E.R.-C. was supported by FEDER/Ministerio de Ciencia e Innovación-Agencia Estatal de Investigación (PID2021-127631NA-I00 and RYC2020-030762-I). V.G.S. was supported by the U.S. Department of Energy Biological Environmental Research Program to UT-Battelle, LLC (DE-AC05-00OR22725) and the NGEE-Arctic project. This paper was reviewed by the USGS, USFS and USEPA for technical and policy content and approved for publication. The views and conclusions in this article represent those of USGS, and represent those solely of the authors from ORAU/ORISE, USFS and USEPA. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government. We thank C. Ely, K. Kavanagh, J. Larison, T. Greaver, A. Gray and M. Brehob.

Author contributions C.R.R.E., S.S.P., D.N.L.M., C.C.C. and S.C.R. led the investigation. C.R.R.E. conducted formal analyses and wrote the first draft with inputs from S.S.P., D.N.L.M., C.C.C. and S.C.R. All authors, C.R.R.E., S.S.P., D.N.L.M., C.C.C., S.C.R., B.N.T., S.A.B., C.M.C., T.E.C., K.A.D., M.G., M.J.G., D.F.H., S.E.J., S.K.-G., M.B.P., J.P., E.R.-C., V.G.S., F.M.S., A.P.S., B.W., C.A.W. and N.W., contributed to methods development, data collection and editing the paper.

Competing interests The authors declare no competing interests.

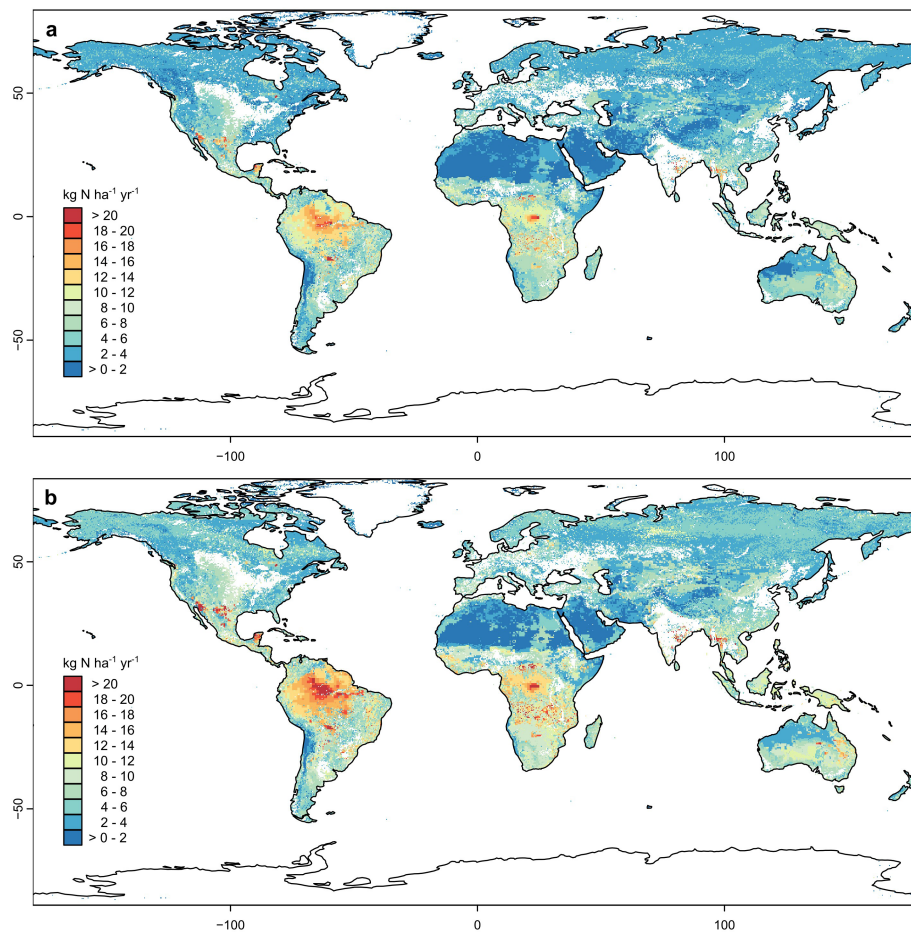
Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41586-025-09201-w>.

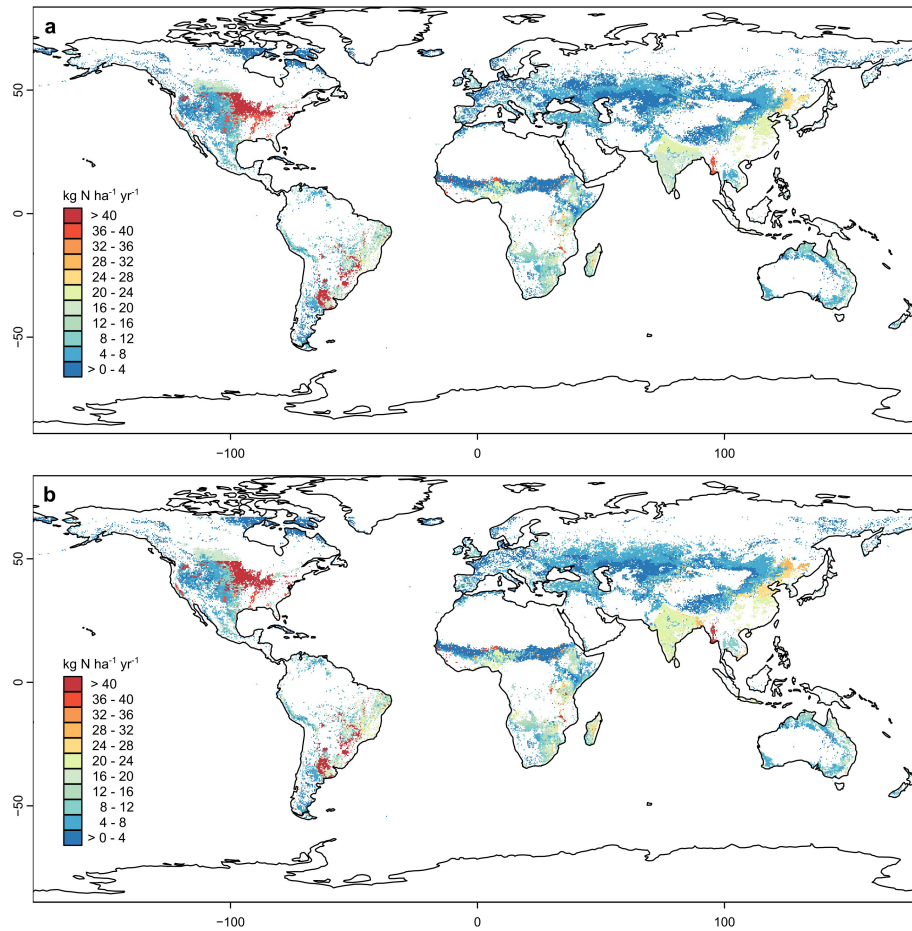
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Peer review information *Nature* thanks Eric Davidson and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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Extended Data Fig. 1 | Confidence interval of natural terrestrial BNF. Total BNF rate ($\text{kg N ha}^{-1} \text{yr}^{-1}$) lower (a) and upper bound (b) 68% confidence interval values (analogous to ± 1 standard error). BNF is mapped across terrestrial lands aside from croplands, urban areas, and areas with permanent snow/ice cover.



Extended Data Fig. 2 | Confidence interval of agricultural BNF. Total BNF rate ($\text{kg N ha}^{-1} \text{yr}^{-1}$) lower (a) and upper bound (b) 68% confidence interval values (analogous to ± 1 standard error). N-fixing crop BNF is mapped across the total land area of croplands (by country) and N-fixing forage BNF is mapped across

the total land area of grasslands between 67°N/S (thus overlapping with natural grasslands in Extended Data Fig. 1), with rates adjusted to total land areas (see details in Methods and Supplementary Methods).

Article

Extended Data Table 1 | Niche-specific estimates of BNF activity per unit of N fixer or N-fixing substrate abundance in natural terrestrial biomes

BNF niche	Unit	ENF	DNF	EBF	DBF	MF	Shrub	Sav	Nat grass	Barren	Wet
Trees	kg N ha ⁻¹ yr ⁻¹ %BA ⁻¹	0.91 (0.80 – 1.01) n = 33	0.73 (0.69 – 0.77) n = 168*	0.65 (0.58 – 0.72) n = 65	0.72 (0.66 – 0.79) n = 57	0.70 (0.58 – 0.82) n = 13	0.18 (0.14 – 0.21) n = 61*	0.18 (0.14 – 0.21) n = 61	ND	ND	ND
Shrubs	kg N ha ⁻¹ yr ⁻¹ %cover ⁻¹	0.55 (0.43 – 0.67) n = 28	0.53 (0.41 – 0.64) n = 29*	0.53 (0.41 – 0.64) n = 29*	0.53 (0.41 – 0.64) n = 29*	0.53 (0.41 – 0.64) n = 29*	0.20 (0.12 – 0.26) n = 11	0.20 (0.14 – 0.27) n = 13*	0.20 (0.14 – 0.27) n = 13*	0.20 (0.14 – 0.27) n = 13*	ND
Herbs	%N _{dif}	87.3 (84.2 – 90.3) n = 3	84.2 (79.6 – 89.0) n = 8*	84.2 (79.6 – 89.0) n = 8*	89.4 (84.9 – 93.9) n = 4	84.2 (79.6 – 89.0) n = 8*	53.9 (49.9 – 58.1) n = 45*	53.9 (49.9 – 58.1) n = 45*	52.1 (47.7 – 56.8) n = 41	53.9 (49.9 – 58.1) n = 45*	ND
Soil	kg N ha ⁻¹ yr ⁻¹	0.65 (0.53 – 0.76) n = 46	1.28 (1.06 – 1.51) n = 117*	2.43 (1.87 – 3.01) n = 38	0.72 (0.36 – 1.08) n = 24	1.08 (0.89 – 1.26) n = 9	0.60 (0.50 – 0.70) n = 5	2.20 (1.78 – 2.64) n = 39*	2.40 (1.88 – 2.98) n = 31	0.11 (0.09 – 0.13) n = 39	1.91 (0.88 – 2.87) n = 12
Litter	kg N ha ⁻¹ yr ⁻¹	0.47 (0.34 – 0.61) n = 28	0.75 (0.67 – 0.84) n = 111*	1.00 (0.87 – 1.15) n = 58	0.39 (0.27 – 0.50) n = 15	0.63 (0.44 – 0.79) n = 10	0.23 (0.13 – 0.33) n = 3	0.14 (0.12 – 0.15) n = 52	0.14 (0.12 – 0.16) n = 55*	0.007 (0.006 – 0.008) n = 55*	ND
Dead wood	mg N kg ⁻¹ yr ⁻¹	13.7 (11.0 – 16.5) n = 30	19.4 (16.1 – 22.8) n = 44*	41.1 (27.6 – 54.6) n = 11	49.1 (39.6 – 58.5) n = 7	22.5 (19.4 – 25.6) n = 44*	39.6 (34.2 – 45.0) n = 48*	30.7 (23.7 – 37.6) n = 48*	ND	ND	ND
Ground mosses	kg N ha ⁻¹ yr ⁻¹ %cover ⁻¹ (x 100)	1.60 (1.15 – 2.07) n = 38	1.58 (1.21 – 1.97) n = 44*	1.58 (1.21 – 1.97) n = 44*	1.58 (1.21 – 1.97) n = 44*	0.99 (0.64 – 1.31) n = 4	6.83 (3.68 – 9.92) n = 6	1.58 (1.21 – 1.97) n = 44*	1.29 (0.69 – 1.90) n = 10	3.37 (1.91 – 4.69) n = 16*	19.70 (15.40 – 24.20) n = 12
Biocrusts	kg N ha ⁻¹ yr ⁻¹ %cover ⁻¹ (x 100)	ND	ND	ND	ND	ND	9.97 (7.39 – 12.50) n = 46	5.11 (3.88 – 6.28) n = 59	12.40 (9.61 – 15.00) n = 30	5.37 (4.18 – 6.58) n = 14	ND
Epiphytic lichens	kg N ha ⁻¹ yr ⁻¹	0.60 (0.45 – 0.76) n = 25*	0.60 (0.45 – 0.76) n = 25*	0.60 (0.45 – 0.76) n = 25*	0.60 (0.45 – 0.76) n = 25*	0.60 (0.45 – 0.76) n = 25*	ND	ND	ND	ND	ND

Values are BNF rates (kg N ha⁻¹ yr⁻¹) per 1% N fixer relative basal area (kg N ha⁻¹ yr⁻¹ %BA⁻¹) for trees, 1% N fixer ground cover (kg N ha⁻¹ yr⁻¹ %cover⁻¹) for shrubs, mosses, and biocrusts, the percent nitrogen derived from the atmosphere (%N_{dif}) for N-fixing herbs, and BNF rates per unit of dry mass (mg N kg⁻¹ yr⁻¹) for dead wood. We used BNF rates per unit of area for epiphytic lichens because BNF rates per unit of N fixer abundance were not available for this niche. We also used BNF rates per unit of area for soil and litter as we do not expect sampling bias regarding substrate abundance for these niches. Central estimates are 2.5% trimmed means and lower and upper bounds in parentheses are 68% confidence intervals (analogous to ± 1 standard error). The “n =” value in each cell indicates the number of BNF activity values upon which the rates in the cell are based. “*” indicates that data was absent or limited, and we substituted data from other biomes to account for niche spatial coverage; see details in Methods and Supplementary Methods. “ND” stands for “Not determined”. ENF = Evergreen needleleaf forests, DNF = Deciduous needleleaf forests, EBF = Evergreen broadleaf forests, DBF = Deciduous broadleaf forests, MF = Mixed forests, Shrub = Shrublands, Sav = Savannas, Nat grass = Natural grasslands, Wet = Permanent wetlands.

Extended Data Table 2 | Niche-specific estimates of BNF activity per unit of N fixer abundance in agricultural systems

BNF niche	Unit	Estimates	Sources
Croplands			
Soybean	%N _{dfa}	Brazil: 78 (76 – 81), n = 7 Europe: 44 (39 – 48), n = 8 Other: 61 (60 – 63), n = 55	ref ^{20,21}
Groundnut	%N _{dfa}	62 (61– 63), n = 156	
Pulses	%N _{dfa}	Africa: 55 (54 – 57), n = 247 Asia: 64 (63 – 65), n = 247 Europe: 63 (62 – 64), n = 247 North America: 58 (57 – 59), n = 247 South America: 42 (41 – 44), n = 247 Oceania: 64 (62 – 65), n = 247	
Cultivated pastures			
Legumes	kg N ha ⁻¹ yr ⁻¹ Mg biomass ⁻¹	43.9 (42.0 – 45.8), n = 84	ref ^{28,29}

Values are the percent nitrogen derived from the atmosphere (%N_{dfa}) for legume crops and BNF rates (kg N ha⁻¹ yr⁻¹) per megagram of N fixer net primary production (kg N ha⁻¹ yr⁻¹ Mg biomass⁻¹) for forage legumes based on the sources listed. Central estimates are arithmetic means and lower and upper bounds in parentheses and 68% confidence intervals (analogous to ± 1 standard error); see details in Methods and Supplementary Methods. “n” indicates the sample size.

Extended Data Table 3 | Summary of current terrestrial BNF rates (kg N ha⁻¹ yr⁻¹) by niche by biome and global totals

	Area [†] (10 ⁹ ha)	Trees	Shrubs	Herbs	Soil	Litter	Dead wood	Ground mosses	Biocrusts	Epiphytic lichens	Sum of niches
Natural terrestrial biomes											
ENF	2.40	1.20 (1.06 – 1.33) n = 33	0.40 (0.31 – 0.49) n = 28	0.22 (0.21 – 0.23) n = 3	0.65 (0.53 – 0.76) n = 46	0.47 (0.34 – 0.61) n = 28	0.18 (0.12 – 0.25) n = 30	0.28 (0.20 – 0.37) n = 38	ND	0.06 (0.04 – 0.07) n = 25*	3.46 (2.82 – 4.10) n = 231
DNF	0.43	0.10 (0.09 – 0.11) n = 168*	0.48 (0.37 – 0.58) n = 29*	0.30 (0.28 – 0.32) n = 8*	1.28 (1.06 – 1.51) n = 117*	0.75 (0.67 – 0.84) n = 111*	0.27 (0.17 – 0.36) n = 44*	0.24 (0.19 – 0.30) n = 44*	ND	0.05 (0.03 – 0.06) n = 25*	3.46 (2.87 – 4.08) n = 546
EBF	12.00	5.34 (4.74 – 5.91) n = 65	1.02 (0.79 – 1.24) n = 29*	0.29 (0.27 – 0.30) n = 8*	2.43 (1.87 – 3.01) n = 38	1.00 (0.87 – 1.15) n = 58	2.20 (1.45 – 2.94) n = 11	0.05 (0.04 – 0.07) n = 44*	ND	0.05 (0.03 – 0.06) n = 25*	12.38 (10.07 – 14.67) n = 278
DBF	2.90	3.87 (3.55 – 4.26) n = 57	0.28 (0.22 – 0.34) n = 29*	0.35 (0.33 – 0.36) n = 4	0.72 (0.36 – 1.08) n = 24	0.39 (0.27 – 0.50) n = 15	0.42 (0.34 – 0.50) n = 7	0.03 (0.03 – 0.04) n = 44*	ND	0.03 (0.03 – 0.04) n = 25*	6.09 (5.12 – 7.12) n = 205
MF	4.71	1.54 (1.27 – 1.81) n = 13	0.22 (0.17 – 0.27) n = 29*	0.18 (0.17 – 0.19) n = 8*	1.08 (0.89 – 1.26) n = 9	0.63 (0.44 – 0.79) n = 10	0.22 (0.18 – 0.27) n = 44*	0.06 (0.04 – 0.07) n = 4	ND	0.05 (0.03 – 0.06) n = 25*	3.97 (3.18 – 4.72) n = 142
Shrub	13.83	0.47 (0.37 – 0.56) n = 61*	0.93 (0.59 – 1.24) n = 11	0.90 (0.83 – 0.97) n = 45*	0.60 (0.50 – 0.70) n = 5	0.23 (0.13 – 0.33) n = 3	0.09 (0.06 – 0.11) n = 48*	0.22 (0.12 – 0.31) n = 6	2.06 (1.53 – 2.58) n = 46	ND	5.49 (4.14 – 6.82) n = 225
Sav	27.54	1.03 (0.82 – 1.24) n = 61	0.65 (0.45 – 0.85) n = 13*	1.74 (1.61 – 1.87) n = 45*	2.20 (1.78 – 2.64) n = 39*	0.14 (0.12 – 0.15) n = 52	0.09 (0.07 – 0.12) n = 48*	0.05 (0.04 – 0.07) n = 59	0.21 (0.16 – 0.26) n = 59	ND	6.11 (5.05 – 7.21) n = 361
Natural grass	22.60	ND	0.40 (0.28 – 0.52) n = 13*	1.78 (1.62 – 1.93) n = 41	2.42 (1.89 – 3.00) n = 31	0.14 (0.13 – 0.16) n = 55*	ND	0.07 (0.04 – 0.10) n = 10	2.34 (1.81 – 2.82) n = 30	ND	7.13 (5.76 – 8.54) n = 180
Barren	20.22	ND	0.10 (0.07 – 0.13) n = 13*	< 0.001 (0.006 – 0.008) n = 45*	0.11 (0.09 – 0.13) n = 39*	0.007 (0.006 – 0.008) n = 55*	ND	< 0.001 n = 16*	1.37 (1.07 – 1.68) n = 14	ND	1.59 (1.23 – 1.95) n = 182
Wet	1.35	ND	ND	ND	1.91 (0.88 – 2.87) n = 12	ND	ND	7.46 (5.83 – 9.16) n = 12	ND	ND	9.37 (6.71 – 12.03) n = 24
Natural biomes	107.99	1.11 (0.96 – 1.27) n = 229	0.53 (0.37 – 0.68) n = 4	0.99 (0.91 – 1.07) n = 53	1.54 (1.21 – 1.89) n = 168	0.26 (0.21 – 0.31) n = 166	0.31 (0.21 – 0.40) n = 48	0.16 (0.12 – 0.21) n = 72	1.06 (0.82 – 1.30) n = 149	0.01 (0.01 – 0.01) n = 25	5.97 (4.81 – 7.15) n = 952
Cultivated pastures											
Legumes	7.94	ND	ND	24.7 (23.6 – 25.8) n = 84	ND	ND	ND	ND	ND	ND	24.7 (23.6 – 25.8) n = 84
Croplands											
Legumes	2.40 [‡]	ND	ND	139.2 (136.3 – 143.7) n = 329	ND	ND	ND	ND	ND	ND	139.2 (136.3 – 143.7) n = 329
Rice	1.61 [‡]	ND	ND	ND	14.6 (11.1 – 18.3) n = 6	ND	ND	ND	ND	ND	14.6 (11.1 – 18.3) n = 6
Sugarcane	0.10 [‡]	ND	ND	49.5 [§] (44.5 – 54.0) n = 9	ND	ND	ND	ND	ND	ND	49.5 [§] (44.5 – 54.0) n = 9

Central estimates are 2.5% trimmed means for natural biomes (Fig. 2a) and arithmetic means for agricultural sources (Fig. 2b) weighted by land area. Lower and upper bounds in parentheses are 68% confidence intervals (analogous to ± 1 standard error) (Extended Data Figs. 1 and 2). The “n =” value in each cell indicates the number of BNF activity values upon which the rates in the cell are based. “*” indicates that data was absent or limited, and we substituted data from other biomes to account for niche spatial coverage; see details in Methods and Supplementary Methods. “ND” stands for “Not determined”. The biome abbreviations are as in Extended Data Table 1. [†]IGBP land cover area in 2019 from ref. 51 - the land area of biomes weighted mean BNF rates across natural biomes. [‡]Cultivated land area of N-fixing crops in 2019 from ref. 37. [§]Data from ref. 53.

Extended Data Table 4 | Summary of current terrestrial BNF inputs (Tg N yr⁻¹) by niche by biome and global totals

	Area† (10 ⁶ ha)	Trees	Shrubs	Herbs	Soil	Litter	Dead wood	Ground mosses	Biocrusts	Epiphytic lichens	Global total
Natural terrestrial biomes											
ENF	2.40	0.29 (0.25 – 0.32) n = 33	0.10 (0.08 – 0.12) n = 28	0.05 (0.05 – 0.06) n = 3	0.16 (0.13 – 0.18) n = 46	0.11 (0.08 – 0.15) n = 28	0.04 (0.03 – 0.06) n = 30	0.07 (0.05 – 0.09) n = 38	ND	0.01 (0.01 – 0.02) n = 25*	0.83 (0.68 – 0.99) n = 231
DNF	0.43	0.004 (0.004 – 0.005) n = 168*	0.02 (0.02 – 0.02) n = 29*	0.01 (0.01 – 0.01) n = 8*	0.06 (0.05 – 0.07) n = 117*	0.03 (0.03 – 0.04) n = 111*	0.01 (0.01 – 0.02) n = 44*	0.01 (0.01 – 0.01) n = 44*	ND	0.002 (0.001 – 0.002) n = 25*	0.15 (0.12 – 0.18) n = 546
EBF	12.00	6.41 (5.69 – 7.09) n = 65	1.23 (0.95 – 1.48) n = 29*	0.34 (0.33 – 0.37) n = 8*	2.91 (2.24 – 3.61) n = 38	1.20 (1.04 – 1.38) n = 58	2.64 (1.74 – 3.53) n = 11	0.06 (0.05 – 0.08) n = 44*	ND	0.05 (0.04 – 0.07) n = 25*	14.86 (12.08 – 17.60) n = 278
DBF	2.90	1.12 (1.03 – 1.23) n = 57	0.08 (0.06 – 0.10) n = 29*	0.10 (0.10 – 0.11) n = 4	0.21 (0.11 – 0.31) n = 24	0.11 (0.08 – 0.14) n = 15	0.12 (0.10 – 0.15) n = 7	0.01 (0.01 – 0.01) n = 44*	ND	0.01 (0.01 – 0.01) n = 25*	1.77 (1.48 – 2.06) n = 205
MF	4.71	0.72 (0.60 – 0.85) n = 13	0.10 (0.08 – 0.13) n = 29*	0.08 (0.08 – 0.09) n = 8*	0.51 (0.42 – 0.59) n = 9	0.30 (0.21 – 0.37) n = 10	0.11 (0.08 – 0.13) n = 44*	0.03 (0.02 – 0.03) n = 4	ND	0.02 (0.02 – 0.03) n = 25*	1.87 (1.50 – 2.22) n = 142
Shrub	13.83	0.64 (0.51 – 0.77) n = 61*	1.29 (0.82 – 1.72) n = 11	1.25 (1.15 – 1.34) n = 45*	0.84 (0.70 – 0.97) n = 5	0.32 (0.18 – 0.46) n = 3	0.12 (0.08 – 0.16) n = 48*	0.30 (0.16 – 0.43) n = 6	2.85 (2.11 – 3.58) n = 46	ND	7.60 (5.72 – 9.43) n = 225
Sav	27.54	2.84 (2.27 – 3.42) n = 61	1.79 (1.24 – 2.35) n = 13*	4.79 (4.44 – 5.16) n = 45*	6.06 (4.89 – 7.28) n = 39*	0.38 (0.33 – 0.42) n = 52	0.26 (0.18 – 0.33) n = 48*	0.14 (0.11 – 0.18) n = 44*	0.58 (0.44 – 0.71) n = 59	ND	16.84 (13.90 – 19.86) n = 361
Natural grass	22.60	ND	0.90 (0.62 – 1.18) n = 13*	4.01 (3.67 – 4.37) n = 41	5.46 (4.28 – 6.78) n = 31	0.32 (0.28 – 0.37) n = 55*	ND	0.15 (0.08 – 0.22) n = 10	5.28 (4.10 – 6.38) n = 30	ND	16.13 (13.02 – 19.30) n = 180
Barren	20.22	ND	0.19 (0.13 – 0.25) n = 13*	0.001 (0.001 – 0.001) n = 45*	0.22 (0.18 – 0.27) n = 39*	0.01 (0.01 – 0.02) n = 55*	ND	< 0.001 (0.79 – 1.24) n = 16*	2.78 (2.16 – 3.40) n = 14	ND	3.21 (2.49 – 3.94) n = 182
Wet	1.35	ND	ND	ND	0.26 (0.12 – 0.39) n = 12	ND	ND	1.01 (0.79 – 1.24) n = 12	ND	ND	1.27 (0.91 – 1.63) n = 24
Natural biomes total	107.99	12.03 (10.35 – 13.69) n = 229	5.70 (4.01 – 7.35) n = 42	10.65 (9.83 – 11.51) n = 53	16.68 (13.10 – 20.45) n = 168	2.79 (2.24 – 3.34) n = 166	3.31 (2.22 – 4.37) n = 48	1.78 (1.27 – 2.30) n = 72	11.48 (8.80 – 14.07) n = 149	0.10 (0.08 – 0.13) n = 25	64.51 (51.90 – 77.20) n = 952
Cultivated pastures											
Legumes	7.94	ND	ND	19.6 (18.8 – 20.5) n = 84	ND	ND	ND	ND	ND	ND	19.6 (18.8 – 20.5) n = 84
Croplands											
Legumes	2.40 [‡]	ND	ND	33.4 (32.7 – 34.5) n = 329	ND	ND	ND	ND	ND	ND	33.4 (32.7 – 34.5) n = 329
Rice	1.61 [‡]	ND	ND	ND	2.3 (1.8 – 2.9) n = 6	ND	ND	ND	ND	ND	2.3 (1.8 – 2.9) n = 6
Sugarcane	0.10 [‡]	ND	ND	0.50 (0.45 – 0.54) n = 9	ND	ND	ND	ND	ND	ND	0.50 (0.45 – 0.54) n = 9

Central estimates are 2.5% trimmed means for natural biomes and arithmetic means for agricultural sources. Lower and upper bounds in parentheses are 68% confidence intervals (analogous to ± 1 standard error). The “n =” value in each cell indicates the number of BNF activity values upon which the rates in the cell are based. “*” indicates that data was absent or limited, and we substituted data from other biomes to account for niche spatial coverage; see details in Methods and Supplementary Methods. “ND” stands for “Not determined”. The biome abbreviations are as in Extended Data Table 1. [†]IGBP land cover area in 2019 from ref. 51. [‡]Cultivated land area of N-fixing crops in 2019 from ref. 37.

Extended Data Table 5 | Summary of N fixer or N-fixing substrate abundance in natural terrestrial biomes

BNF niche	Unit	ENF	DNF	EBF	DBF	MF	Shrub	Sav	Nat grass	Barren	Wet	Global mean
Trees	Relative basal area (%)	1.22	0.14	8.37	4.73	1.75	8.80	5.10	ND	ND	ND	3.41
Shrubs	Ground cover (%)	0.73	0.90*	1.93	0.52	0.42	4.74	3.18	1.93	0.47	ND	2.18
Herbs	Relative ground cover (%)	2.35	2.03*	2.87	1.57	1.34	3.77	5.63	4.83	0.26	ND	3.46
Soil	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Litter	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Dead wood	Biomass (Mg ha ⁻¹)	15.7	16.5	53.4	23.0	17.1	5.7	3.1	ND	ND	ND	37.9
Mosses	Ground cover (%)	17.77	15.33	3.34	2.12	5.57	3.15	3.31	5.12	0.004	37.90	3.92
Biocrusts	Ground cover (%)	ND	ND	ND	ND	ND	14.86	3.50	17.10	24.71	ND	9.41
Epiphytic lichens	Plots with abundant N-fixing cyanolichens (%)	9.37	7.47*	7.47*	5.58	7.47*	ND	ND	ND	ND	ND	6.22

Values are arithmetic means calculated as described in Methods and Supplementary Methods based on sources listed in Supplementary Table 1. “*” indicates that data were absent or limited, and we substituted data from other biomes to account for niche spatial coverage. No abundance datasets were used for soil and litter as we do not expect sampling bias regarding substrate abundance for these niches. “NA” stands for “Not applicable”. “ND” stands for “Not determined”. The biome abbreviations are as in Extended Data Table 1. The land area of biomes (Extended Data Table 3) weighted global mean abundances across natural biomes. Uncertainty estimates are not shown due to a lack of clarity on the true number of independent degrees of freedom in each BNF niche in each biome, but the uncertainty of the abundance data are generally much lower than the uncertainty of BNF rate data (Extended Data Table 1). For example, standard errors of the global means of the abundance of N-fixing trees, shrubs, herbs, and biocrusts are all ≤ 0.01 .

Extended Data Table 6 | Alternative calculation of current terrestrial BNF rates (kg N ha⁻¹ yr⁻¹) using the assumptions in ref. 3

Biome	Area† (10 ⁶ ha)	Trees	Shrubs	Herbs	Soil	Litter	Dead wood	Ground mosses	Biocrusts	Epiphytic lichens	Sum of niches
ENF	2.40	10.07 (8.96 – 11.09) n = 37	4.77 (3.99 – 5.61) n = 45	0.14 (0.09 – 0.18) n = 3	0.54 (0.46 – 0.62) n = 32	0.35 (0.28 – 0.43) n = 25	0.87 (0.70 – 1.03) n = 30	1.74 (0.83 – 2.60) n = 17	ND	0.60 (0.45 – 0.76) n = 25*	19.09 (17.46 – 20.71) n = 214
DNF	0.43	6.61 (6.15 – 7.06) n = 187*	3.75 (2.72 – 4.74) n = 65*	0.28 (0.17 – 0.38) n = 7*	1.35 (1.06 – 1.62) n = 90*	0.68 (0.60 – 0.77) n = 98*	0.99 (0.85 – 1.14) n = 56*	1.44 (0.82 – 2.05) n = 24*	ND	0.60 (0.45 – 0.76) n = 25*	15.69 (14.36 – 17.01) n = 552
EBF	12.00	4.22 (3.64 – 4.76) n = 76	0.95 (0.74 – 1.17) n = 6	0.28 (0.17 – 0.38) n = 7*	2.41 (1.67 – 3.12) n = 33	0.94 (0.79 – 1.10) n = 49	1.02 (0.82 – 1.22) n = 25*	1.44 (0.82 – 2.05) n = 24*	ND	0.60 (0.45 – 0.76) n = 25*	11.86 (10.70 – 13.02) n = 245
DBF	2.90	7.12 (6.27 – 8.12) n = 58	1.74 (1.34 – 2.18) n = 12	0.38 (0.16 – 0.61) n = 4	0.94 (0.49 – 1.38) n = 18	0.39 (0.27 – 0.50) n = 15	1.07 (0.86 – 1.28) n = 14*	1.44 (0.82 – 2.05) n = 24*	ND	0.60 (0.45 – 0.76) n = 25*	13.70 (12.38 – 15.02) n = 167
MF	4.71	8.13 (6.39 – 9.98) n = 16	3.75 (2.72 – 4.74) n = 65*	0.28 (0.17 – 0.38) n = 7*	1.03 (0.80 – 1.26) n = 7	0.61 (0.41 – 0.81) n = 9	0.99 (0.85 – 1.14) n = 56*	0.81 (0.51 – 1.11) n = 5	ND	0.60 (0.45 – 0.76) n = 25*	16.20 (14.08 – 18.31) n = 130
Shrub	13.83	2.26 (1.80 – 2.76) n = 61*	3.70 (2.60 – 4.66) n = 19	0.33 (0.21 – 0.45) n = 4	0.62 (0.62 – 0.63) n = 3	0.23 (0.13 – 0.33) n = 3	0.29 (0.17 – 0.39) n = 7*	4.18 (1.99 – 6.32) n = 9*	12.76 (8.08 – 17.40) n = 10	ND	24.37 (19.10 – 29.64) n = 116
Sav	27.54	2.26 (1.80 – 2.76) n = 61	3.77 (2.96 – 4.63) n = 24*	0.07 (0.05 – 0.08) n = 51	3.23 (2.51 – 3.86) n = 20*	0.14 (0.12 – 0.15) n = 52	0.29 (0.17 – 0.39) n = 7*	1.44 (0.82 – 2.05) n = 24*	0.43 (0.19 – 0.65) n = 60	ND	11.62 (10.26 – 12.97) n = 299
Natural grass	22.60	ND	3.77 (2.96 – 4.63) n = 24*	1.91 (1.70 – 2.14) n = 34	3.69 (2.90 – 4.61) n = 17	0.14 (0.12 – 0.16) n = 55*	ND	1.19 (0.56 – 1.75) n = 7	12.02 (7.70 – 16.40) n = 11	ND	22.72 (18.16 – 27.27) n = 148
Barren	20.22	ND	0.19 (0.15 – 0.23) n = 24*	0.04 (0.03 – 0.05) n = 89*	0.16 (0.13 – 0.19) n = 20*	0.007 (0.006 – 0.008) n = 55*	ND	0.21 (0.10 – 0.32) n = 9*	3.94 (2.67 – 5.22) n = 10	ND	4.55 (3.27 – 5.83) n = 207
Wet	1.35	ND	ND	ND	4.14 (2.33 – 6.23) n = 5	ND	ND	12.55 (9.27 – 16.10) n = 15	ND	ND	16.69 (12.75 – 20.62) n = 20
Natural biomes	107.99	2.13 (1.77 – 2.51) n = 248	2.70 (2.07 – 3.33) n = 89	0.52 (0.43 – 0.61) n = 96	2.12 (1.63 – 2.60) n = 115	0.25 (0.20 – 0.30) n = 153	0.28 (0.19 – 0.35) n = 56	0.69 (0.40 – 0.98) n = 48	4.15 (2.66 – 5.65) n = 91	0.13 (0.09 – 0.16) n = 25	12.96 (9.44 – 16.50) n = 921

This table presents alternative calculations to illustrate how assumed N fixer abundances in ref. 3 yield biased BNF rates. Central estimates are 2.5% trimmed means and lower and upper bounds in parentheses are 68% confidence intervals (analogous to ± 1 standard error). BNF by trees, shrubs, and herbs were adjusted to an assumed N fixer cover of 15%, the overall mid-range value used in ref. 3. The “n =” value in each cell indicates the number of BNF activity values upon which the rates in the cell are based. “*” indicates that data was absent or limited, and we substituted data from other biomes to account for niche spatial coverage; see details in Methods and Supplementary Methods. “ND” stands for “Not determined”. The biome abbreviations are as in Extended Data Table 1. †IGBP land cover area in 2019 from ref. 51 - the land area of biomes weighted global mean BNF rates across natural biomes.

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Extended Data Table 7 | Alternative calculation of current terrestrial BNF inputs (Tg N yr⁻¹) using the assumptions in ref. 3

Biome	Area ^a (10 ⁶ ha)	Trees	Shrubs	Herbs	Soil	Litter	Dead wood	Ground mosses	Biocrusts	Epiphytic lichens	Global total
ENF	2.40	2.42 (1.15 – 2.67) n = 37	1.15 (0.96 – 1.35) n = 45	0.03 (0.02 – 0.04) n = 3	0.13 (0.11 – 0.15) n = 32	0.09 (0.07 – 0.10) n = 25	0.21 (0.17 – 0.25) n = 30	0.42 (0.20 – 0.62) n = 17	ND	0.14 (0.11 – 0.18) n = 25*	4.59 (3.77 – 5.38) n = 214
DNF	0.43	0.29 (0.27 – 0.31) n = 187*	0.16 (0.12 – 0.21) n = 65*	0.01 (0.01 – 0.02) n = 7*	0.06 (0.05 – 0.07) n = 90*	0.03 (0.03 – 0.03) n = 98*	0.04 (0.04 – 0.05) n = 56*	0.06 (0.04 – 0.09) n = 24*	ND	0.03 (0.02 – 0.03) n = 25*	0.68 (0.55 – 0.81) n = 552
EBF	12.00	5.06 (4.37 – 5.70) n = 76	1.14 (0.88 – 1.40) n = 6	0.33 (0.10 – 0.45) n = 7*	2.90 (2.00 – 3.74) n = 33	1.13 (0.95 – 1.32) n = 49	1.22 (0.99 – 1.46) n = 25*	1.72 (0.99 – 2.46) n = 24*	ND	0.72 (0.54 – 0.91) n = 25*	14.23 (10.83 – 17.56) n = 245
DBF	2.90	2.06 (1.82 – 2.35) n = 58	0.51 (0.39 – 0.63) n = 12	0.11 (0.05 – 0.18) n = 4	0.27 (0.14 – 0.40) n = 18	0.11 (0.08 – 0.14) n = 15	0.31 (0.25 – 0.37) n = 14*	0.42 (0.24 – 0.60) n = 24*	ND	0.18 (0.13 – 0.22) n = 25*	3.97 (3.07 – 4.91) n = 167
MF	4.71	3.83 (3.01 – 4.70) n = 16	1.77 (1.28 – 2.34) n = 65*	0.13 (0.08 – 0.18) n = 7*	0.49 (0.38 – 0.59) n = 7	0.29 (0.19 – 0.38) n = 9	0.47 (0.40 – 0.54) n = 56*	0.38 (0.24 – 0.52) n = 5	ND	0.28 (0.21 – 0.36) n = 25*	7.63 (5.77 – 9.53) n = 130
Shrub	13.83	3.13 (2.49 – 3.82) n = 61*	5.12 (3.59 – 6.45) n = 19	0.46 (0.30 – 0.62) n = 4	0.86 (0.85 – 0.87) n = 3	0.32 (0.18 – 0.46) n = 3	0.40 (0.23 – 0.54) n = 7*	1.77 (0.85 – 2.69) n = 9*	12.23 (7.74 – 16.68) n = 10	ND	24.28 (16.23 – 32.12) n = 116
Sav	27.54	6.23 (4.06 – 7.60) n = 61	10.38 (8.15 – 2.74) n = 24*	0.18 (0.14 – 0.21) n = 51	8.90 (6.92 – 10.63) n = 20*	0.38 (0.33 – 0.42) n = 52	0.32 (0.19 – 0.45) n = 7*	0.66 (0.38 – 0.94) n = 24*	0.99 (0.44 – 1.49) n = 60	ND	28.03 (21.50 – 34.49) n = 299
Natural grass	22.60	ND	8.52 (6.69 – 10.46) n = 24*	4.31 (3.83 – 4.85) n = 34	8.35 (6.56 – 10.42) n = 17	0.32 (0.28 – 0.36) n = 55*	ND	0.32 (0.15 – 0.47) n = 7	23.96 (15.35 – 32.69) n = 11	ND	45.77 (32.85 – 59.25) n = 148
Barren	20.22	ND	0.38 (0.30 – 0.47) n = 24*	0.08 (0.07 – 0.09) n = 89*	0.33 (0.25 – 0.39) n = 20*	0.01 (0.01 – 0.02) n = 55*	ND	0.02 (0.01 – 0.02) n = 9*	7.67 (5.19 – 10.16) n = 10	ND	8.48 (5.84 – 11.15) n = 207
Wet	1.35	ND	ND	ND	0.56 (0.32 – 0.84) n = 5	ND	ND	1.70 (1.25 – 2.18) n = 15	ND	ND	2.26 (1.57 – 3.02) n = 20
Natural biomes total	107.99	23.03 (19.07 – 27.15) n = 248	29.12 (22.36 – 35.95) n = 89	5.64 (4.69 – 6.64) n = 96	22.84 (17.58 – 28.11) n = 115	2.67 (2.12 – 3.24) n = 153	2.97 (2.10 – 3.82) n = 56	7.46 (4.33 – 10.58) n = 48	44.84 (28.73 – 61.01) n = 91	1.35 (1.01 – 1.71) n = 25	139.92 (101.98 – 178.21) n = 921

This table presents alternative calculations to illustrate how assumed N fixer abundances in ref. 3 yield biased BNF rates. Central estimates are 2.5% trimmed means and lower and upper bounds in parentheses are 68% confidence intervals (analogous to ± 1 standard error). BNF by trees, shrubs, and herbs were adjusted to an assumed N fixer cover of 15%, the overall mid-range value used in ref. 3. The “n=” value in each cell indicates the number of BNF activity values upon which the rates in the cell are based. “*” indicates that data was absent or limited, and we substituted data from other biomes to account for niche spatial coverage; see details in Methods and Supplementary Methods. “ND” stands for “Not determined”. The biome abbreviations are as in Extended Data Table 1. ^aIGBP land cover area in 2019 from ref. 51.

Extended Data Table 8 | Summary of pre-industrial terrestrial BNF inputs (Tg N yr⁻¹) by niche by biome and global total

Biome	Area [†] (10 ⁸ ha)	Trees	Shrubs	Herbs	Soil	Litter	Dead wood	Ground mosses	Biocrusts	Epiphytic lichens	Global total
ENF	5.47	0.61 (0.54 – 0.67)	0.22 (0.17 – 0.27)	0.12 (0.11 – 0.12)	0.36 (0.29 – 0.42)	0.26 (0.16 – 0.33)	0.11 (0.07 – 0.15)	0.18 (0.13 – 0.24)	ND	0.31 (0.23 – 0.39)	1.88 (1.51 – 2.23)
DNF	2.12	0.02 (0.02 – 0.02)	0.10 (0.08 – 0.12)	0.07 (0.06 – 0.07)	0.27 (0.22 – 0.32)	0.16 (0.14 – 0.18)	0.06 (0.04 – 0.08)	0.06 (0.04 – 0.07)	ND	0.01 (0.01 – 0.01)	0.74 (0.61 – 0.88)
EBF	16.82	9.12 (8.10 – 10.10)	1.72 (1.34 – 2.08)	0.50 (0.47 – 0.53)	4.09 (3.15 – 5.06)	1.69 (1.46 – 1.94)	3.68 (2.43 – 4.91)	0.09 (0.07 – 0.11)	ND	0.08 (0.06 – 0.10)	20.96 (17.05 – 24.81)
DBF	2.57	0.88 (0.81 – 0.97)	0.07 (0.06 – 0.09)	0.09 (0.08 – 0.09)	0.19 (0.09 – 0.28)	0.10 (0.07 – 0.13)	0.11 (0.09 – 0.13)	0.01 (0.01 – 0.01)	ND	0.01 (0.01 – 0.01)	1.45 (1.21 – 1.70)
MF	16.49	2.01 (1.66 – 2.36)	0.37 (0.28 – 0.44)	0.27 (0.26 – 0.29)	1.78 (1.46 – 2.08)	1.03 (0.72 – 1.29)	0.38 (0.29 – 0.47)	0.11 (0.07 – 0.14)	ND	0.07 (0.06 – 0.09)	6.02 (4.79 – 7.17)
Shrub	30.76	4.74 (3.79 – 5.71)	2.86 (1.82 – 3.82)	2.88 (2.67 – 3.10)	1.86 (1.55 – 2.17)	0.71 (0.40 – 1.02)	0.22 (0.14 – 0.30)	1.07 (0.58 – 1.56)	4.56 (3.38 – 5.72)	ND	18.90 (14.33 – 23.39)
Sav	19.27	1.72 (1.38 – 2.08)	1.26 (0.87 – 1.64)	3.10 (2.87 – 3.34)	4.24 (3.42 – 5.10)	0.26 (0.23 – 0.30)	0.16 (0.11 – 0.21)	0.16 (0.12 – 0.20)	0.24 (0.26 – 0.42)	ND	11.25 (9.27 – 13.28)
Natural grass	16.38	ND	0.65 (0.45 – 0.85)	2.09 (1.91 – 2.27)	3.93 (3.08 – 4.88)	0.23 (0.20 – 0.26)	ND	0.16 (0.09 – 0.24)	2.54 (1.97 – 3.07)	ND	9.60 (7.70 – 11.58)
Barren	18.27	ND	0.18 (0.12 – 0.23)	0.05 (0.04 – 0.05)	0.20 (0.16 – 0.24)	0.01 (0.01 – 0.02)	ND	< 0.001	2.42 (1.89 – 2.97)	ND	2.86 (2.22 – 3.51)
Natural biomes total	128.16	19.10 (16.28 – 21.90)	7.42 (5.19 – 9.54)	9.15 (8.48 – 9.86)	16.91 (13.43 – 20.54)	4.45 (3.42 – 5.46)	4.72 (3.16 – 6.24)	1.84 (1.10 – 2.57)	9.86 (7.49 – 12.18)	0.20 (0.15 – 0.25)	73.65 (58.70 – 88.54)

Central estimates are 2.5% trimmed means and lower and upper bounds in parentheses are 68% confidence intervals (analogous to ± 1 standard error). Pre-industrial BNF inputs were based on current biome simple means of grid cell values of BNF rate (kg N ha⁻¹ yr⁻¹) for each niche; see Methods and Supplementary Methods for details. “ND” stands for “Not determined”. The biome abbreviations are as in Extended Data Table 1. [†]IGBP land cover area in the year 1500 CE from ref. 64.

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The global gridded BNF rate datasets generated as results of this study and the BNF rate dataset underlying our estimates in natural terrestrial biomes are available in the ScienceBase repository using the DOIs provided in the main text. All other data are available from the databases cited or are in the main text, extended data, or supplementary materials.

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Study description	We develop new estimates of global terrestrial biological nitrogen fixation by upscaling field measurements of biological nitrogen fixation rates using rigorously quantified, spatially explicit abundances of all major nitrogen fixing niches in natural terrestrial and agricultural systems to map the global distribution and estimate biome and global totals of biological nitrogen fixation fluxes for each niche.
Research sample	Our dataset includes 1,177 field measurements of biological nitrogen fixation rates for nitrogen-fixing trees, shrubs, and herbs, and in association with soil, litter, dead wood, mosses, lichens, and biocrusts in natural terrestrial biomes. Our dataset also includes 5,557 field measurements of biological nitrogen fixation in legume crop, legume forage, rice, and sugarcane systems. Our dataset also assembles data on nitrogen fixer and nitrogen-fixing substrate abundances from various global, regional, and national sources.
Sampling strategy	We used systematic keyword searches in main search engines to access field measurements of terrestrial biological nitrogen fixation rates published globally. Our analysis includes more than four times rate data than previous bottom-up global syntheses.
Data collection	All data was assembled manually into spreadsheet templates. Data on nitrogen fixer and nitrogen-fixing substrate abundances was obtained from published datasets, global and regional databases, and national inventories. We used data from unmanaged and managed ecosystems (e.g., silviculture/forestry, rangelands, and agroforestry systems) to upscale biological nitrogen fixation rates in natural terrestrial biomes and data from grain croplands and pastures intensively managed for forage/livestock production to upscale biological nitrogen fixation rates in agricultural biomes.
Timing and spatial scale	Field measurements of terrestrial biological nitrogen fixation rates from the literature were conducted between 1952 and 2018, with the majority of the data (60%) measured between 2000 and 2018. The spatial scale is global.
Data exclusions	We excluded data from recent clear-cuts and young plantations (< 1 year old) in natural biomes due to more intense human disturbance. We also excluded data for pure cultures of N-fixing prokaryotes isolated from field samples, as these do not represent nitrogen fixing activity in the presence of a symbiont and/or community.
Reproducibility	Literature search was conducted once. Each data entry was checked against its original publication, with particular attention to whether potential outliers represented data entry errors. Each data analysis step was checked at least twice to ensure the results were consistent.
Randomization	We grouped data into nitrogen fixation niches as classified by authors in the original sources or based on global databases. We also grouped data into biome types using the vegetation descriptions and classifications from the original sources and the International Geosphere-Biosphere Program (IGBP) land cover system.
Blinding	Blinding was not possible in our study. We used systematic approaches for data collection and analysis to avoid bias in results.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Plants

Seed stocks

not applicable

Novel plant genotypes

not applicable

Authentication

not applicable