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Deforestation impacts soil biodiversity and ecosystem services worldwide

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Deforestation poses a global threat to biodiversity and its capacity to deliver ecosystem services. Yet, the impacts of deforestation on soil biodiversity and its associated ecosystem services remain virtually unknown. We generated a global dataset including 696 paired-site observations to investigate how native forest conversion to other land uses affects soil properties, biodiversity, and functions associated with the delivery of multiple ecosystem services. The conversion of native forests to plantations, grasslands, and croplands resulted in higher bacterial diversity and more homogeneous fungal communities dominated by pathogens and with a lower abundance of symbionts. Such conversions also resulted in significant reductions in carbon storage, nutrient cycling, and soil functional rates related to organic matter decomposition. Responses of the microbial community to deforestation, including bacterial and fungal diversity and fungal guilds, were predominantly regulated by changes in soil pH and total phosphorus. Moreover, we found that soil fungal diversity and functioning in warmer and wetter native forests is especially vulnerable to deforestation. Our work highlights that the loss of native forests to managed ecosystems poses a major global threat to the biodiversity and functioning of soils and their capacity to deliver ecosystem services.

global scale | forest conversion | fungal guilds | microbial diversity | meta-analysis

Native forests are critical for the biodiversity and functioning of terrestrial ecosystems and support of multiple ecosystem services worldwide (1). However, native forests have gone through dramatic changes over the last few centuries due to human population growth and accelerating rates of deforestation worldwide (2). This includes conversion from native forests to grasslands, croplands, and plantations for the provision of food and industrial raw materials (3). In the tropics, for example, agriculture-driven deforestation alone reached 6.4 to 8.8 million hectares per year between 2011 and 2015 (2), and in southern Chile, 30% of native temperate forests were lost between 1985 and 2011 alone due to the expansion of exotic tree plantations (4). While the impacts of forest deforestation on above-ground biomass and biodiversity have been a major research focus for decades (5–7), remarkably little is known about deforestation impacts on soil biodiversity and functions associated with the delivery of multiple ecosystem services across the globe (8).

To date, most studies exploring the impact of deforestation on soil biodiversity and functions have focused on single types of ecosystem conversion (e.g., from forest to cropland) or on selected soil ecosystem properties, such as carbon (C) storage (6, 9, 10). As such, integrative studies considering the multiple dimensions of soil biodiversity and functions, and their responses to changes in land use types, are lacking. Soil microorganisms regulate many ecosystem functions, including litter decomposition, pathogen control, and nutrient mineralization and uptake by plants (11, 12). Thus, alterations to soil biodiversity affect the performance of soil functions, and the delivery of ecosystem services, simultaneously. Converted ecosystem types differ in vegetation diversity and management, with croplands being the most different to native forests and the most intensively managed. These land use differences lead us to predict that the responses of soil biodiversity and functions to changes in land use will vary considerably between forest conversion types (12). Deforestation would also lead to contrasting changes on microbial groups in soil due to their fundamental differences in physiology and life history (13, 14). For example, native forest ecosystems often support a greater abundance of symbiotic fungi due to high vegetation diversity and biomass, while host-specific pathogens are more likely to dominate fungal communities in managed systems, such as intensive croplands, with high host density (15–17). Most studies on native forest conversion have been conducted at local to regional scales (9, 10), and we lack a global assessment that considers the impact of multiple factors, including soil abiotic properties, climate, forest conversion types, on biodiversity change under deforestation. Taken together, these knowledge gaps hamper our ability to predict changes in soil ecosystem services after deforestation and

Significance

Deforestation alters aboveground biodiversity and ecosystem services worldwide. Yet, the impacts of deforestation on soil biodiversity, and its associated ecosystem services, remain virtually unknown. Our global synthesis indicates that deforestation of native forest impacts soil biodiversity and the capacity to support ecosystem services. Conversion of native forests to managed ecosystems resulted in soils with reduced capacity to support soil-borne plant pathogen regulation, plant–soil symbiosis, carbon storage, nutrient cycling, and organic matter decomposition. Soil biodiversity and functions were most negatively affected when native forests were converted to cropland and in warmer and wetter ecosystems. Our work highlights the fundamental importance of avoiding soil degradation caused by deforestation to conserve soils and the services they provide for the next generations.

The authors declare no competing interest.

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to develop conservation strategies to protect soil biodiversity and function (18).

Here, we collected a global database including 696 pairs of native forest conversion to plantation, grassland, and cropland from 154 studies, using space for time substitution, to investigate the responses of multiple measures of soil biodiversity and function to deforestation (Fig. 1). Our study includes a wide range of soil properties, microbial diversity and functions associated with soil biodiversity, and key ecosystem services such as C sequestration, nutrient cycling, organic matter decomposition, plant–soil symbiosis, and pathogen control (see *SI Appendix*, Table S1 and Dataset S1, for a complete list of soil variables). The number of paired observations depended on the particular soil variable studied as acknowledged in *SI Appendix*, Table S1. Our study provides, to our knowledge, the most complete global database to investigate the impacts of deforestation on different aspects of soil conservation. In our study, we considered the conversion of native forests to a wide range of land uses, including plantations, grasslands, and croplands, across a wide range of forest types and climatic regions (tropical, subtropical, and temperate forests). This allowed us to reveal the detailed effects of forest conversion on soil biodiversity and functions associated with important ecosystem services globally and assess the role of abiotic factors in controlling these complex soil microbial responses (1, 19).

We hypothesize that i) the conversion from native forests to managed systems results in critical changes in multiple soil variables (soil properties, microbial diversity, and functions; *SI Appendix*, Table S1) across a global environmental gradient, leading to more homogenous, pathogen dominated soil communities, supporting reduced levels of key ecosystem services (e.g., soil C, nutrient cycling, organic matter decomposition, plant–soil symbiosis; *SI Appendix*, Table S1); ii) due to its more intensive land management, conversion from native forest to cropland has the most negative impact on multiple soil variables associated with soil properties, biodiversity, and functions than conversion to other land use types; and iii) changes in soil biodiversity after native forest conversion may be driven by parallel changes in soil abiotic factors and conversion types, with subsequent impacts for the maintenance of soil biodiversity and function.

Results and Discussion

Deforestation Led to Critical Reductions in Soil Ecosystem Services. Our work revealed that the conversion from native forests to plantations, grasslands, and croplands has critical impacts on soil properties and results in the reduction of key ecosystem services, including soil C storage and nutrient cycling (Fig. 2*A* and *SI Appendix*, Fig. S3). Generally, deforestation caused major declines (30% on average across sites) in soil organic C (Fig. 2*A*). This soil organic C loss was substantial (≈24%) when forests were converted to tree plantations or grasslands. These grasslands are, of course, relatively young grasslands which may have a reduced capacity to capture carbon in their soils compared with older and well-developed grasslands (14, 20). Importantly, loss of soil C was especially strong after forest conversion to croplands, which reduced by 48%. Decreases in net primary productivity with forest conversion are the most important reason for soil organic C losses due to reductions in C input from plant material (6, 21). The increase of soil erosion with the decrease of plant cover in managed ecosystems also accelerates soil C loss (1, 22). The decline in soil organic C content after forest conversion was equally strong across all biomes, suggesting that deforestation impact on soil C sequestration is a global problem.

The decreasing trend of soil total nitrogen (N) after forest conversion was also substantial (23%) (Fig. 2*A*). Deforestation resulted in a substantial decline in soil C:N, with particularly strong reductions when forest was converted to cropland (Fig. 2*A*). Thus, native forest conversion led to a greater decline in soil C storage than in soil N, which is likely related to the input of N fertilizers in managed ecosystems and the decrease of lignified and recalcitrant C in litter caused by the shift from woody plants to grasses after deforestation (12, 13). The reduction of C:N ratio with deforestation was also associated with a major shift in the structure and functions of the soil microbial community, increasing the growth of fast-turnover

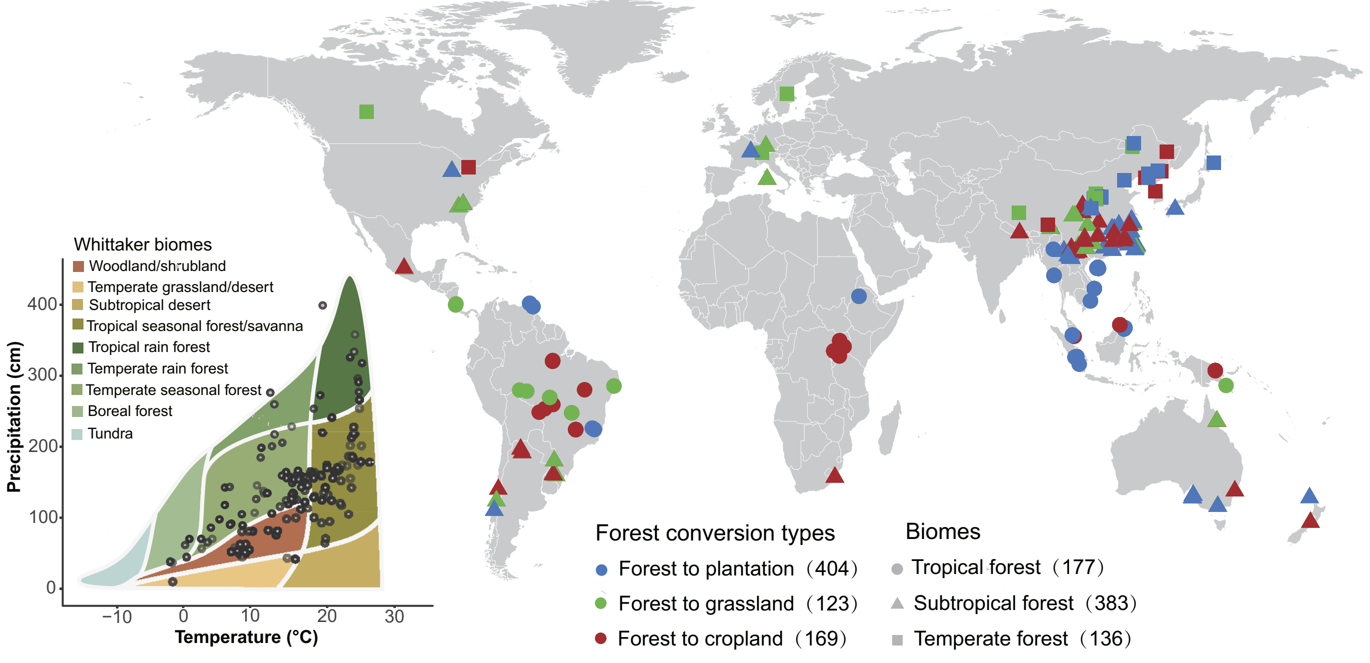

Fig. 1. Global distribution of study sites including conversions from native forests to plantations, grasslands, and croplands. Colors represent forest conversion types, and shapes represent biomes. The numbers in brackets show the number of data pairs (forest vs. converted ecosystems). The *Left Inset* represents the distribution of study sites within main biomes.

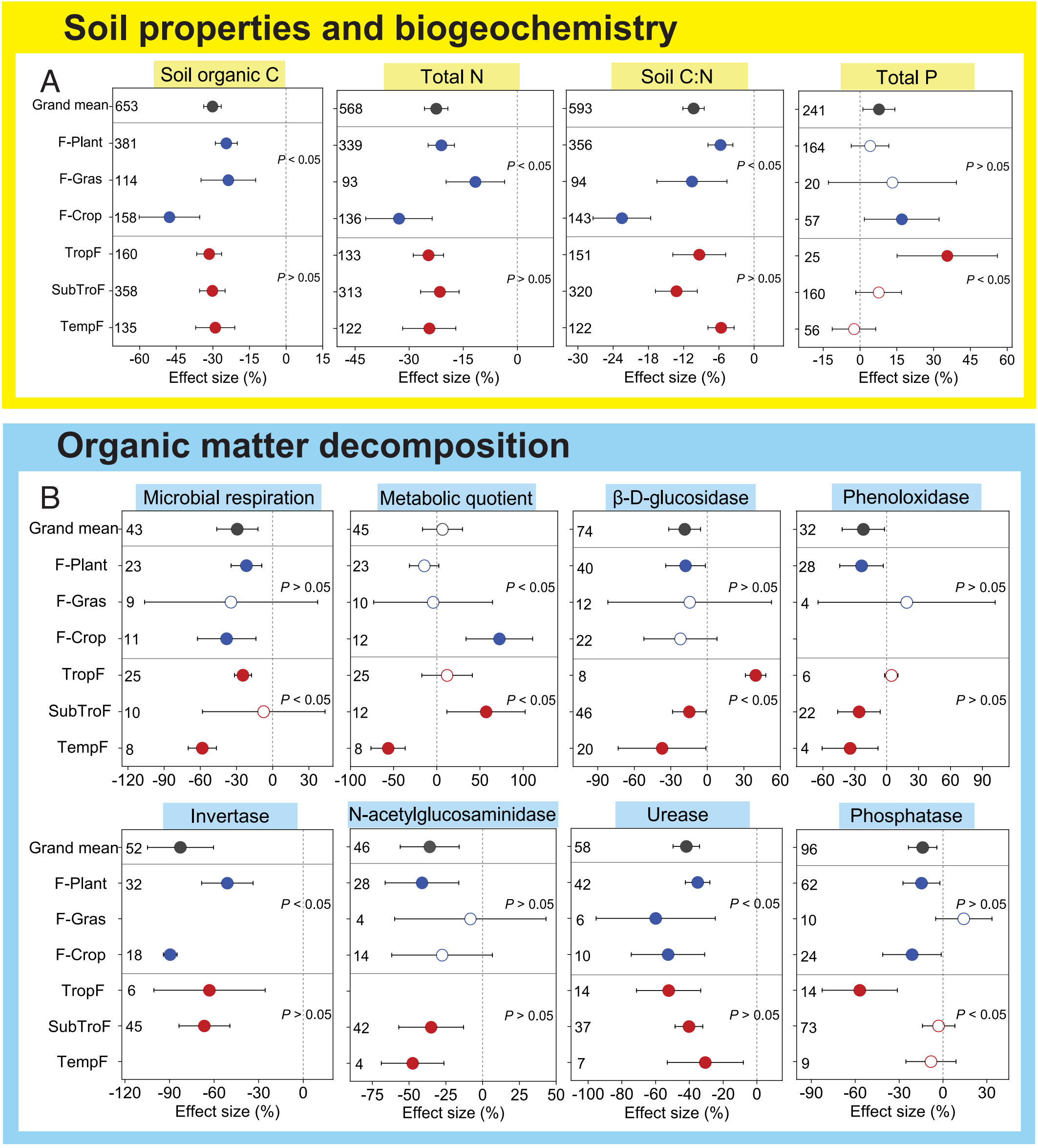

Fig. 2. Effects of native forest conversion on (*A*) soil properties/nutrient cycling (biogeochemistry) and (*B*) proxies of soil organic matter decomposition. Values are effect size ±95% CI. F-Plant, F-Gras, and F-Crop represent native forest conversion to plantation, to grassland, and to cropland, respectively. TropF, SubTroF, and TempF represent tropical forest, subtropical forest, and temperate forest, respectively. The sample size in each category is given at the *Left*. The closed symbols indicate significant effects, and the open symbols indicate nonsignificant effects. The difference between categories is significant if $P < 0.05$.

bacteria, but negatively affecting taxa capable of degrading complex organic compounds (Figs. 2 and 3) (13, 21).

Native forest conversion to managed systems also increased soil pH, especially when converted to croplands and grasslands, and in tropical biomes (*SI Appendix*, Fig. S3). Meanwhile, soil phosphorus (P) content increased with deforestation (Fig. 2*A* and *SI Appendix*, Fig. S3), which is mainly due to the intensive use of P fertilizers in managed systems. A reduction in soil acidity, as observed in our analysis, is known to release insoluble-P from mineral complexes, and is another likely mechanism for the increase of soil available P after deforestation (23). In general, reductions in soil organic C storage, changes in soil properties and fertilizer inputs after forest conversion to managed ecosystems lead to changes in soil C:N:P (22), which are linked to the impacts on microbial diversity and ecosystem functions, such as plant–soil symbiosis and pathogen control.

Native forest conversion to managed systems also limited biologically driven processes involved in soil organic matter decomposition. The functional rates related to organic matter decomposition and C, N and P mineralization, including soil microbial respiration, β-D-glucosidase, phenoloxidase, invertase, N-acetylglucosaminidase, urease, and phosphatase activities, all significantly decreased after deforestation (Fig. 2*B*). Moreover, native forest conversion to plantation limited the rate of soil functioning to a similar extent as does conversion to grassland and cropland. This result extends and validates previous assessments that compositionally simpler plantations used for wood and nonwood products are much less effective than complex native forests in maintaining soil ecosystem services (1). It is worth noting that, the reduction of C inputs from litterfall, rhizodeposition, and fine root turnover due to decreased ecosystem productivity after deforestation would also presumably support less microbial taxa to decompose organic matter. A previous study has shown a 28% decline in litterfall input from native forest to plantation alone (21) but did not examine the effects of more land use–intensive conversions to cropland or grassland. Thus, the declines in both soil C content and functional capacity related to organic matter decomposition of managed ecosystems indicate that the degradation of soil ecosystem functions after deforestation is difficult to restore.

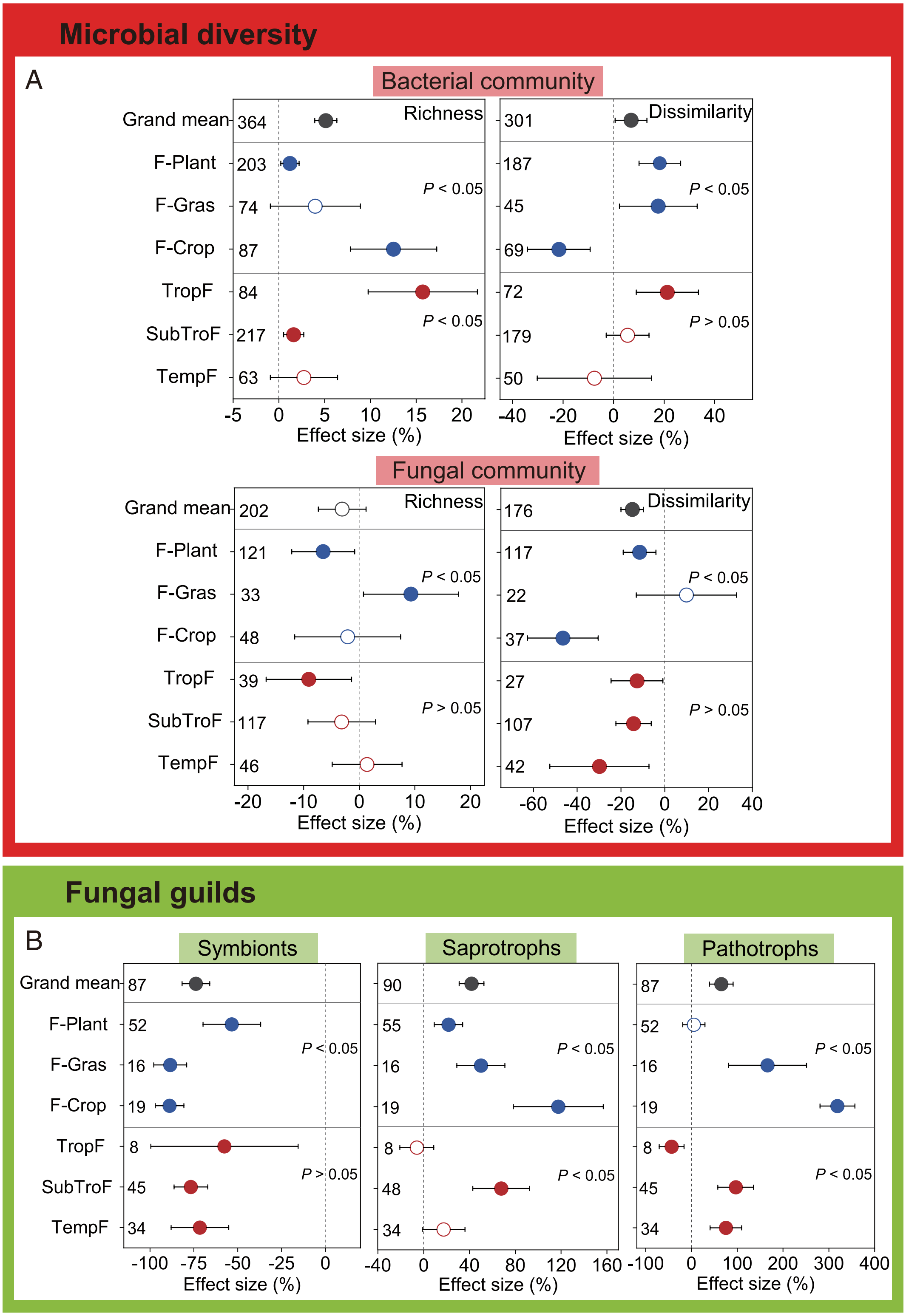

Fig. 3. Effects of native forest conversion on soil biodiversity: (*A*) microbial diversity and (*B*) fungal guilds. Values are mean effect size ± 95% CI. F-Plant, F-Gras, and F-Crop represent native forest conversion to plantation, to grassland, and to cropland, respectively. TropF, SubTroF, and TempF represent tropical forest, subtropical forest, and temperate forest, respectively. The sample size in each category is given at the *Left*. The closed symbols indicate significant effects, and the open symbols indicate nonsignificant effects. The difference between categories is significant if $P < 0.05$.

Environmental Context Associated with Forest Conversion Type and Changes in Soil Abiotic Factors Explained Shifts in Microbial Communities Following Deforestation. Native forests conversion to managed ecosystems also had critical impacts on soil microbial diversity (Fig. 3 and *SI Appendix*, Figs. S4–S6). Environmental context linked with forest conversion type and associated changes in abiotic factors explained the influence of deforestation on soil microbial structure and functions (*SI Appendix*, Figs. S5 and S6). First, our analyses revealed that deforestation resulted in a significant increase in bacterial diversity (Fig. 3*A* and *SI Appendix*, Fig. S4), suggesting that managed ecosystems following anthropogenic disturbance support the growth of bacteria with rapid turnover

(12, 14). We further showed that conversion of native forests to croplands and in tropical biomes resulted in the greatest increase in bacterial richness (Fig. 3*A*). Using multiple linear regression and model selection, we found that these responses were associated with parallel changes in key abiotic factors such as an increase in soil pH (Fig. 4*A* and *SI Appendix*, Fig. S5 and Table S2). In fact, soil pH was the most important predictor of soil bacterial richness after deforestation based on the sum of Akaike weights (*SI Appendix*, Fig. S5*A*). The increase of soil pH is caused by decreased vegetation biomass and bedrock rejuvenation, but also by the agricultural practice of liming, which is common for croplands, plantations, and to some extent in grasslands. Increasing soil pH may be especially important during the deforestation of conifers, which are known to acidify soils. Most bacterial species prefer neutral soils and have a narrow range of pH adaptation (24), and thus their diversity increases with pH after forest conversion. Moreover, intensive management practices (e.g., tillage, fertilization, and irrigation) used in croplands are also known to increase bacterial richness (12, 14).

The effects of forest conversion on fungal richness varied with the conversion types (Fig. 3*A*). Native forests converted to grasslands had a less negative effect on fungal richness than to other land use types. This can be attributed to the fact that grasslands are mostly used for grazing and typically have high vegetation diversity relative to other conversion types. Also, manures produced by livestock, which function as organic fertilizer, can expand the functional niche for fungi (25), thereby enhancing their richness. It has been reported that P-deficient soils in natural ecosystems often support the growth of microbial taxa with the ability to decompose organic matter and obtain P at the expense of other microorganisms possessing different functions (26, 27). The change of fungal richness after native forest conversion was positively associated with soil total P (Fig. 4*B* and *SI Appendix*, Fig. S5*B* and Table S2), indicating that the mitigation of P-deficiency in managed systems alleviates its restriction for microbial taxa with diverse functions. However, this does not inherently represent a positive phenomenon in terms of ecosystem function, as higher fungal richness caused by increased soil P content after deforestation is more likely to increase the diversity of pathogens rather than beneficial taxa, with implications for the functioning of these ecosystems (17).

Our results also showed that deforestation led to a decline in fungal community dissimilarity, although the extent depended on forest conversion type (Fig. 3*A* and *SI Appendix*, Fig. S5*B*). Both fungal and bacterial community dissimilarities were lower in croplands compared to native forests (Fig. 3*A*), indicating that agricultural intervention led to homogenization of soil microbial communities (14). The homogeneity of communities in managed ecosystems is likely a result of the loss of endemic microorganisms from native forests and/or an increase in the ranges of existing taxa, which alters the delivery of soil ecosystem services (6, 14). In general, after forest conversion, ecosystems were dominated by bacteria and more homogeneous fungal communities challenging the conservation of native soils globally.

Effects of native forest conversion on soil biodiversity also translated into important taxonomic changes. The bacterial communities of managed ecosystems included a larger proportion of Bacteroidetes, Gemmatimonadetes, Firmicutes, Chloroflexi, and Nitrospriae but had a reduced abundance of Proteobacteria, Acidobacteria, and Verrucomicrobia (*SI Appendix*, Fig. S7). The fungal community after deforestation supported a larger proportion of Ascomycota at the expense of decreasing Basidiomycota abundance (*SI Appendix*, Fig. S8). These shifts of microbial taxa after native forest conversion were also related to the increase in soil pH and total P (*SI Appendix*, Fig. S9). Changes of community composition can also help explain differences in soil ecosystem functions and services. For example, the decline of Proteobacteria with deforestation, which contains a variety of beneficial bacteria that promote plant growth and protection against diseases, could negatively affect ecosystem productivity (28).

Our study also revealed that climate is an important factor influencing the response of soils to the forest conversion (*SI Appendix*, Fig. S6 and Table S3). Mean annual temperature (MAT) and aridity index (AI) were negatively correlated with the change of fungal richness, but positively correlated with the change of bacterial richness in response to forest conversion (*SI Appendix*, Fig. S6). These changes were related to the decline in fungal richness, and the increase in bacterial richness in response to forest conversion, which were most pronounced in tropical biomes (Fig. 3*A*). These results indicated that deforestation has a greater negative effect on fungal diversity in warmer and wetter ecosystems, but supports the growth of fast-turnover bacteria, thereby contributing to a shift from fungi-dominated to bacteria-dominated microbial communities (12). Fungi exhibited lower richness and higher community dissimilarity in warmer and wetter native ecosystems, which accelerates the loss of fungal endemic species after deforestation (6, 8, 13). In contrast, the survivability for bacteria experiencing higher temperatures, greater precipitation, and environmental disturbance suggests that they are much more likely to dominate managed ecosystems in warmer and wetter areas (13). Moreover, MAT was negatively correlated with the response of organic matter decomposition, including N-acetylglucosaminidase (chitin degradation), urease (urea hydrolysis), and phosphatase (P mineralization) to deforestation (*SI Appendix*, Fig. S6). This suggested that climate can largely regulate the response of soil functions to deforestation.

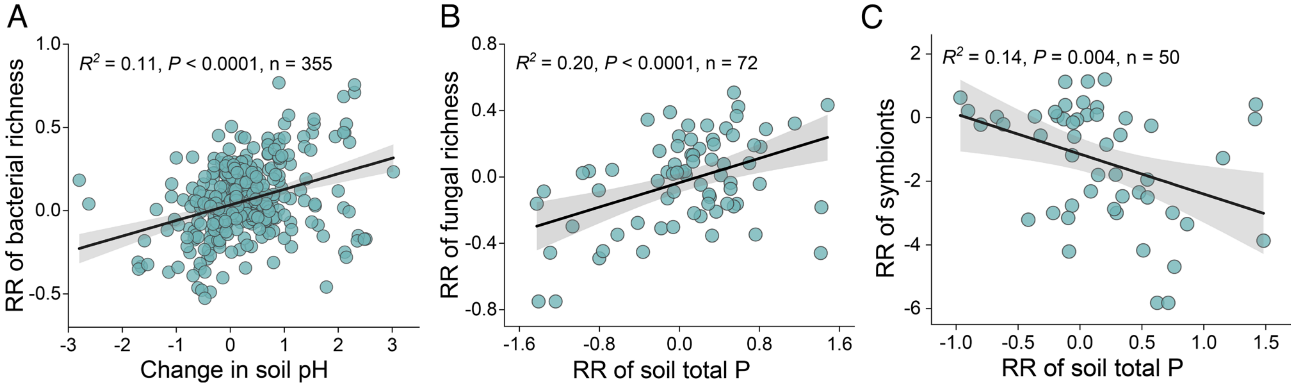

Fig. 4. Mixed effects meta-regression analyses for the relationships between response ratios (RRs) of key soil properties and microbial diversity. RR is calculated from the natural logarithm-transformed ratio of treatment (converted ecosystem) to control (native forest). The gray area represents the 95% CI. Panels *A*–*C* represent regressions between different microbial and soil attributes.

Deforestation Promotes Soil Fungal Plant Pathogens and Reduces Fungal Symbionts. Our analyses provided further evidence that conversion from native forests to managed systems negatively impacted the capacity of ecosystems to support plant–soil symbiosis, with a significant decline in the proportion of symbiotic fungi (Fig. 3*B*) and increase in the proportion of soil-borne plant fungal pathogens. This shift of fungal guilds from symbiont-dominated (e.g., plant–soil symbiosis service) to soil-borne plant pathogen-dominated (e.g., less plant pathogen control) was influenced by land use, with the most pronounced shift occurring after conversion to croplands (Fig. 3*B* and *SI Appendix*, Fig. S5*C*). The decrease of vegetation diversity after deforestation, especially when converted to croplands, where monocultures prevail, results in the losses of symbiotic fungal species that have strong host specificity and limited functional breadth (15). In contrast, the increased density of specific hosts in managed systems may promote the colonization and accumulation of host-dependent fungal pathogens (16, 17). The increase in the abundance of soil-borne plant pathogens strongly increases the risk of host-specific disease, which is detrimental to ecosystem health and limits productivity, especially in croplands (16).

Considering soil properties, P input in managed ecosystems is the most important factor that negatively affects plant–soil symbiosis (Fig. 4*C* and *SI Appendix*, Fig. S5*C*). This outcome may be attributed to high P availability, which decreases plant reliance on symbiotic fungi and increases direct uptake of P by plant roots, resulting in a weakened symbiotic relationship that reduces ecosystem stability and stress resistance (27). We also observed an increase in the abundance of saprotrophs (e.g., decomposers) under native forest conversion (Fig. 3*B*). There is a competitive relationship between decomposers and symbiotic fungi, especially in native forest ecosystems where ectomycorrhizal fungi with decomposition ability dominate the community (29). Thus, the weakening of plant–soil symbiosis after deforestation contributes to a relative increase in decomposers. Nevertheless, the increase in decomposer abundance under deforestation does not imply an increase in decomposing capacity of organic matter, because the saprophytic taxa supported by disturbed and nutrient-rich environments may not have a greater decomposition ability than those in native forest ecosystems (30). Taken together, these results reveal that native forest conversion to managed ecosystems, in particular to croplands, weakens the capacity for plant–soil symbiosis and increases the abundance of pathogens, which poses a long term threat to ecosystem health and functioning.

Linking Soil Biodiversity and Functions Following Forest Conversion. Through mixed-effects linear regression analysis, we found that changes in soil biodiversity following native forest conversion to managed ecosystems influenced the response of soil functional rates related to organic matter decomposition (Fig. 5 and *SI Appendix*, Fig. S10). The effect of deforestation on soil organic matter decomposition was determined by evaluating the changes in eight microbial ecosystem functions (i.e., linked with the decomposition of soil organic matter) using a random-effect model in each paired-site observation (native forest vs. deforestation) (Fig. 2*B*) (18). We show that the response of soil organic matter decomposition to deforestation was negatively correlated with fungal richness (Fig. 5*A*), and that functions associated with chitin degradation (N-acetylglucosaminidase), urea hydrolysis (urease) and P mineralization (phosphatase) were negatively related to bacterial richness (*SI Appendix*, Table S4). This is likely attributed to dramatic changes of microbial community structure after deforestation, specifically through the loss of critical functional taxa (14, 18). For example, the response of organic matter decomposition to deforestation was positively correlated with the abundance of symbiotic fungi and negatively correlated with the abundance of fungal pathogens (Fig. 5 *B* and *C*). This indicated that the shift in fungal guilds from symbiont-dominated to pathogen-dominated following deforestation reduced the functional rate of soil organic matter decomposition. The weakening of plant–soil symbiosis reduces the ability of key fungal taxa to secrete extracellular enzymes to decompose organic matter or acquire N and P to promote plant growth. In contrast, the accumulation of pathogens threatens ecosystem productivity and ultimately fed back to the decline of soil organic matter content and ecosystem functions (15, 16). These results suggest that changes in microbial diversity and the loss of key taxa after native forest conversion negatively affect organic matter decomposition, leading to more abiotic-driven soil with reduced functionality.

Spatial and Temporal Influence of Forest Conversion on Soil Biodiversity and Ecosystem Services. We then attempted to better understand the influence of land use conversion age on soil biodiversity and functionality. To such an end, we categorized the available information in our dataset into three land use age ranges: ≤10 y, 10 to 30 y, and ≥30 y. The results revealed that the observed microbial community shift, from fungal-dominated to bacterial-dominated communities with a decline of plant–soil symbiosis, decreased with the increase of stand age, and recovered to levels similar to native forest after long-term (≥30 y) conversion (*SI Appendix*, Fig. S11). However, soil organic C content and C:N were lower throughout the entire land use age range after conversion (*SI Appendix*, Fig. S12). The homogenization of fungal communities and the shift of fungal guilds from symbiotic-dominated to saprophytic- and pathogenic-dominated were exaggerated with the increase of land use age from native forest to cropland (*SI Appendix*, Fig. S11). In the medium to

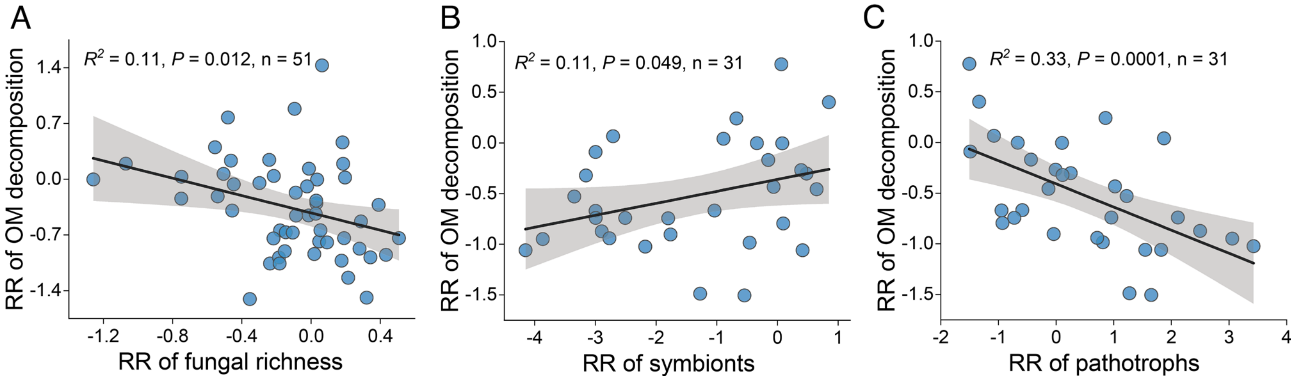

Fig. 5. Mixed effects meta-regression analyses for the relationships between the response ratios (RRs) of microbial diversity and soil organic matter decomposition after native forest conversion. RR is calculated from the natural logarithm-transformed ratio of treatment (converted ecosystem) to control (native forest). RR of OM decomposition is the overall RR of eight functions associated with organic matter decomposition in each observation. OM, organic matter. The gray area represents the 95% CI.Panels *A*–*C* represent regressions between different microbial and soil attributes.

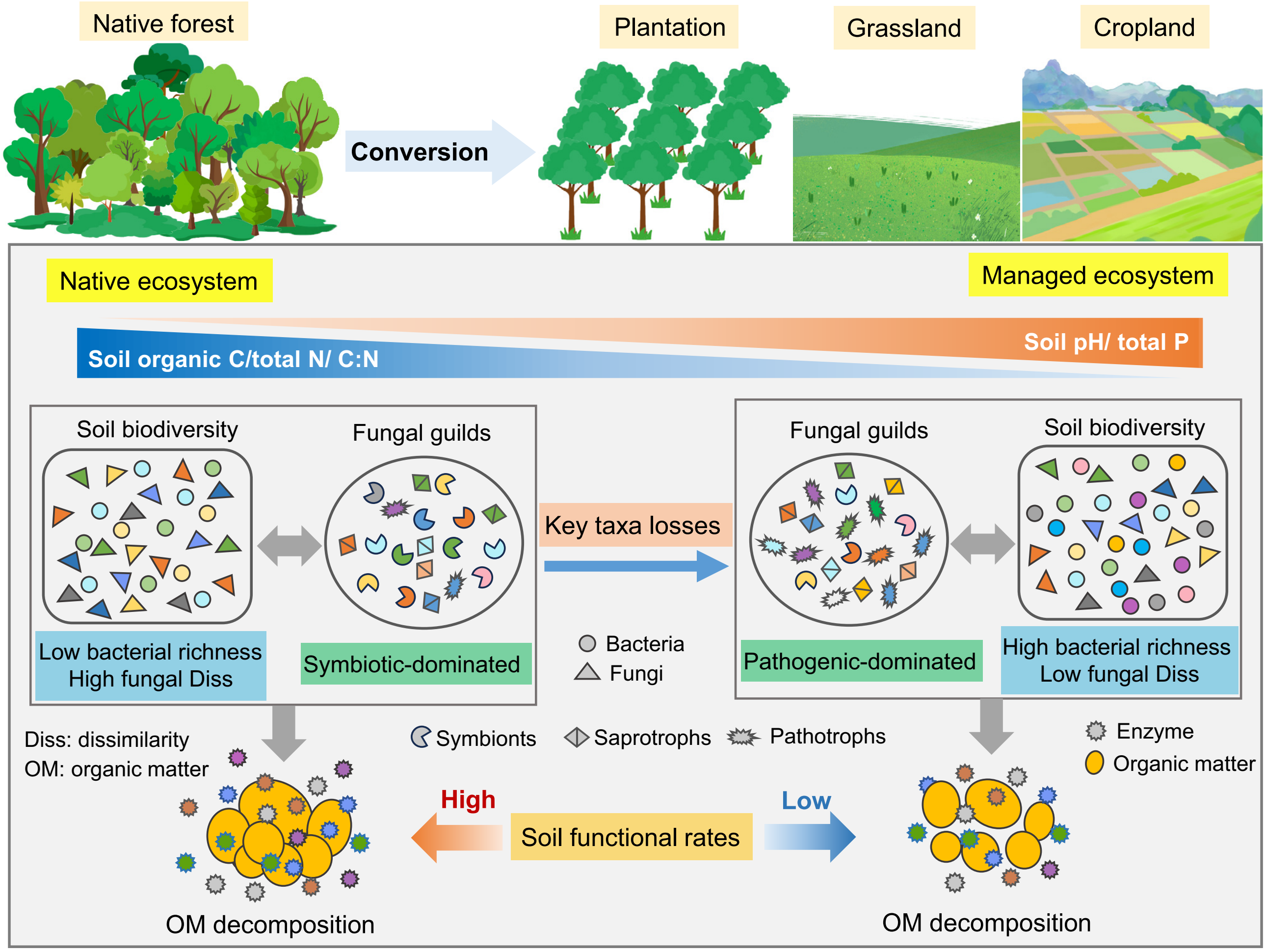

Fig. 6. Conceptual model illustrating the impacts of native forest conversion to other land use types on soil properties, microbial community, and functions.

long term (>10 y) of converted cropland, the proportion of fungal pathogens was five times higher than that in native forest. The decrease of soil C:N and the accumulation of P and potassium also increased with the increase of land use age of cropland (*SI Appendix*, Fig. S12). These results suggested that intensive management of cropland has far greater adverse effects on soil functioning and health in the long term after conversion than other land use types.

Finally, we would like to acknowledge the limitations of our study. It is known that the space for time substitution method has some confounding factors caused by environmental variation across sampling sites that could affect the validity of the results. To mitigate these potential variables in our global analysis, the literature included in the meta-dataset were field experiments that maintained a strict paired-site design. Managed ecosystems and native forest control plots were always adjacent to each other with the same climate (MAT and AI) and soil conditions (of the same soil classification). While there is potential for some factors to differ between native forests and converted ecosystems, such as slope and aspect, their impact on soil microbial communities relative to those resulting from drastic changes in land use is presumed to be relatively small.

Conclusion

In brief, our findings are of high significance because they provide consistent evidence that deforestation of native forest threatens global soil biodiversity and its capacity to provide ecosystem services. The conversion of native forests to managed ecosystems consistently resulted in soils with higher bacterial diversity and more homogeneous fungal communities dominated by pathogens, and these changes are associated with reductions in functions that support important ecosystem services, including carbon storage, nutrient cycling, and organic matter decomposition (Fig. 6). Soil biodiversity and functions are most negatively affected when native forests are converted to croplands and in warmer and wetter ecosystems. When considering abiotic factors, the changes of microbial diversity and fungal guilds in response to deforestation were mainly influenced by soil pH and total P content. Deforestation of native forests, driven by agricultural expansion and land intensification, continues to occur at a rapid pace, especially in tropical regions and developing countries (3, 7). Thus, governments and decision-makers should develop and follow conservation strategies to avoid soil degradation caused by deforestation of native forests. Meanwhile, restoring biodiversity and soil ecosystem services in managed ecosystems is also an important strategy to alleviate the conflicts between human and nature brought about by deforestation and achieve global Sustainable Development Goals (8, 31).

Materials and Methods

Data Collection.

Literature search. We constructed a global database to investigate the responses of multiple soil variables (soil properties, microbial diversity, and function) to deforestation. Peer-reviewed literature related to soil microbial impacts following forest conversion was searched using the Web of Science and China National Knowledge Infrastructure (CNKI) considering all articles until December 1st, 2022 (*SI Appendix*, Fig. S1 for PRISMA diagram). The keywords used in the search were soil AND (microbial community OR bacterial community OR fungal community) AND (forest OR forest conversion OR forest transformation OR land-use change). In our search, we focused on soil microbes as 1) there is a huge gap of knowledge on how soil microbes respond to deforestation and 2) to provide a balanced dataset considering both soil microbes and associated soil properties and functions, which are often simultaneously measured in these studies.

Relevant publications were retained based on the following criteria: 1) Studies were conducted with a paired-site design using space for time substitution approach under field conditions. The paired sites were adjacent, with the same climate and soil conditions (belonging to the same type in the same soil classification system). 2) The reference ecosystem (procedure control) was a native forest that had been naturally developed as a primary or secondary forest. The converted ecosystems included at least one type of plantation, grassland, and cropland. 3) At least one microbial community metric, including alpha diversity (OTU/ASV, Chao, ACE, or Shannon index), beta diversity (community dissimilarity), fungal guilds, or community composition (bacteria or fungi at the phylum level), was reported. 4) The microbial community was quantified by using high-throughput sequencing with Illumina or 454 platform. 5) If the study was conducted over multiple years, measurements from the latest sampling were used, and if the study involved multiple sampling times within 1 year, data for the growing season were used.

Our search resulted in a meta-dataset of 696 paired global observations (Fig. 1) from 154 peer-reviewed studies and our field sampling across southern China, which included multiple soil variables associated with soil properties, microbial diversity and functions (*SI Appendix*, Table S1 and Dataset S1 for a complete list of soil variables and metadata). The experimental data of our sampled soils were shown in Data S1 and the raw sequences of soil bacteria and fungi were deposited in the NCBI Sequence Read Archive under accession numbers PRJNA1033779 and PRJNA1033814, respectively.

Extracted data. We collected multiple soil variables including soil microbial diversity (as explained above), soil ecosystem properties, and functions in our literature search. See *SI Appendix*, Table S1 for a complete list of soil variables and number of observations, along with their connection with specific ecosystem services (e.g., soil carbon, biogeochemistry, organic matter decomposition, plant–soil symbiosis, pathogen control). These raw data were extracted from the text, tables, figures, and supplementary materials of the collated publications. When results were shown in figures, the relevant data were extracted using GetData software (http://getdata-graph-digitizer.com/). We expected to use these data to explore changes of microbial diversity under native forest conversion and its drivers at the global scale, as well as the impact of these changes on ecosystem functions.

For all variables, the mean ($\overline{X}$), SD, and sample size (n) were extracted from publications. If the studies reported SE of the variables, the SD was calculated using the formula SD = SE × $\sqrt{n}$. If a study did not report the SD or SE values, one-tenth of the mean was assigned as the SD (32). We also collected information on location (longitude and latitude), forest conversion type, and biome. If the publication reported the time of managed ecosystems since native forest conversion, we collected this information and named it as land use age. Mean annual temperature (MAT) and mean annual precipitation (MAP) were extracted from the WorldClim database (www.worldclim.org/data/bioclim.html) using geographical coordinates of the study sites. To get a more accurate picture of ecosystem moisture availability, we also extracted the aridity index (AI) from the Global Aridity Index and Potential Evapotranspiration Climate database (https://cgiarcsi.community/) using geographical coordinates of the study sites. In all the collected datasets, three conversion types were classified, as follows: native forest to plantation (F-Plant), to grassland (F-Gras), and to cropland (F-Crop). The native forests were categorized into three biomes, i.e., tropical forest (TropF), subtropical forest (SubTroF), and temperate forest (TempF), based on climate zone division by the Köppen classification system (33). We also categorized the land use age of managed systems into three ranges: short term (≤10 y), medium term (10 to 30 y), and long term (≥30 y). The functional rate related to soil organic matter decomposition was not categorized using age ranges due to the limited sample sizes.

Additional Details on the Collected Data.

Microbial alpha diversity. Microbial richness (number of OTUs/ASVs) and Shannon index are the most commonly used metrics of alpha diversity (18, 34). We thus used these metrics as our preferred diversity indexes. When not available, we used other commonly used metrics such as Chao and ACE indexes.

Microbial community dissimilarity. Microbial community dissimilarity (i.e., microbial composition heterogeneity), was calculated as the averaged Euclidean distance across samples from OTU/ASV relative abundance matrices (8, 18). We extracted the coordinate points in the two-dimensional ordination plots of microbial beta diversity which was calculated based on OTU/ASV relative abundance available from each publication of our meta-analysis search (Dataset S1 and ref. 18). The Euclidean distances within the native forest (procedure control; D_c) and deforested (converted ecosystem) treatment (D_t) of each paired site were calculated using the R *vegan* package (*SI Appendix*, Fig. S13). Then, the means, SDs, and sample sizes of D_c and D_t were calculated at each paired site and were used to calculate the response ratio and variance as described in the Data analyses section. To account for any sample size differences across sites, we included "sample size" in our models while calculating the response ratio and variance between the control (native forest) and treatment (converted ecosystem).

Fungal guilds. If articles reported the relative abundance of three fungal functional groups, e.g., symbionts (e.g., plant–soil symbiosis), saprotrophs (i.e., decomposers), and pathotrophs (e.g., soil-borne plant pathogens), we collected them directly. Otherwise, we downloaded the raw sequences from the National Center for Biotechnology Information (NCBI) based on the accession numbers provided by articles in the metadata. In order to maintain similarity across papers used in this meta-analysis, these raw fungal sequences were clustered into operational taxonomic units (OTUs) at a 97% similarity (35). Representative sequences of each fungal OTU were selected for taxonomic assignment through the UNITE database (36). Then, we performed functional annotation in the FungalTraits database using the genus-level classification of the fungal OTUs (37). We calculated the relative abundances (proportion) of three fungal functional groups, symbiotrophs, saprotrophs, and pathotrophs, and investigate their responses to deforestation.

Soil available nutrients. The literature used many different methods to measure soil available N (AN), available P (AP), available K (AK) content. We collected them according to the following standards. Hydrolysable N content measured by the alkali diffusion method was preferentially collected as soil AN. Otherwise, we collected the ammonium N and nitrate N content measured after extraction by potassium chloride or pure water and calculated the sum of them as the AN. We collected soil AP content that measured after extraction by Bray, Olsen or Mehlich methods. For AK content, we collected the data that determined after extraction by ammonium acetate or Mehlich methods. We do not make any claim about these methods being ideal for measuring nutrient availability. We collected data available from the literature wherein original authors claim to have measured nutrient availability.

Organic matter decomposition. We collected information on eight enzyme activities and soil process rates associated with organic matter decomposition and nutrient cycling: microbial respiration, metabolic quotient, phenol oxidase (oxidize phenols using oxygen), β-D-glucosidase (hydrolyze cellobiose and cellulose oligomers to glucose), invertase (hydrolyze sucrose to fructose and glucose), N-acetylglucosaminidase (chitin degradation), urease (hydrolyze urea to ammonia), and phosphatase (organic P mineralization). These metrics are good surrogates of processes driving soil organic matter decomposition or nutrient cycling driven by microbial communities. We used a random-effect model (formulas are as follows) to calculate the overall effect size of deforestation on eight microbial ecosystem functions associated with organic matter decomposition (i.e., eight functions in Fig. 2*B*) in each paired-site observation (native vs. deforested forest) (18).

Data Analyses.

Calculating the individual response ratios of multiple soil variables to forest conversion. The effect of forest conversion on each observation was calculated using the natural logarithm-transformed (ln) RR:

$$\mathrm{RR} = \ln\left(\frac{x_t}{x_c}\right) = \ln\left(x_t\right) - \ln\left(x_c\right), \qquad [\mathbf{1}]$$

where $\overline{X}_t$ and $\overline{X}_c$ are the means of each variable under the deforested ecosystem (forest conversion) and native forest (procedure control), respectively. The effect of forest conversion on soil pH was expressed as change in soil pH ($\overline{X}_t$-$\overline{X}_c$) (18), because pH itself is a logarithmic scale. The variance (v) of RR was calculated as:

$$v = \frac{S_t^2}{n_\mathrm{t} - \overline{X}_t^2} + \frac{S_c^2}{n_\mathrm{c} - \overline{\mathrm{X}}_\mathrm{c}}, \qquad [\mathbf{2}]$$

where s_t and s_c are the SD of the variable under the converted ecosystem and forest control conditions, respectively; and n_t and n_c are the sample sizes of the variable under the treatment and control conditions, respectively.

Calculation of the overall response ratio and subgroup analysis. To determine whether forest conversion had significant effects on soil variables, random-effects model with maximum-likelihood (ML) estimation was used to calculate overall weighted RR (RR_{++}) and 95% CI. Unlike the fixed-effect model assuming that all studies share a common effect size, the random-effects model allow the response ratio varies from study to study and can also effectively eliminate the effects of heterogeneity in the calculation process (38, 39). In random-effects, the observed mean (Y_i) of each study is given by:

$$Y_i = \mu + \zeta_i + \varepsilon_i, \tag{3}$$

where μ is grand mean, ζ_i is the difference between the true mean (θ_i) for study i and the μ, and ε_i is the difference between Y_i and θ_i. Thus, the random-effects included two sources of variance, one is within-study variance (v_i) from ε_i and the other is between-study variance (τ^2) from ζ_i. It is noted that v_i is unique to each study, but τ^2 is common to all studies (38). The inverse variance scheme was used to assigned the weight (W_i) to each study:

$$W_i = \frac{1}{v_i + \tau^2}. \tag{4}$$

The overall RR_{++} was calculated as:

$$\mathrm{RR}++ = \frac{\sum_{i=1}^{k} W_i Y_i}{\sum_{i=1}^{k} W_i}. \tag{5}$$

The variance (V) of RR_{++} is also the inverse of the weight, which was calculated as:

$$V = \frac{1}{\sum_{i=1}^{k} W_i}. \tag{6}$$

Their 95% CI was calculated as:

$$95\,\%\,\mathrm{CI} = \mathrm{R}_{++} \pm 1.96 \times \sqrt{V}. \tag{7}$$

If the 95% CI values of RR_{++} did not overlap zero, the effect of forest conversion on a variable was considered significant ($P < 0.05$). Subgroup analysis was then conducted to examine the response of multiple soil variables to conversion types and biomes. Between-group heterogeneity tests (Q_m) were used to compare the responses of variables to forest conversion types and biomes among subgroup responses. A significant Q_m ($P < 0.05$) indicated that the response ratios differed among categorical factors (40). All of these analyses were conducted in OpenMEE software (41). We also converted the RR_{++} to a percentage form (except soil pH) to better visualize the response of variables to forest conversion:

$$\text{Effect size (\%)} = [\exp(\mathrm{RR}_{++}) - 1] \times 100\%. \tag{8}$$

Publication bias of each variable was tested using funnel plots and fail-safe analysis. Symmetrical variable distribution in a "funnel" shape around RR_{++}, and the fail-safe number larger than 5k+10 indicate absence of publication bias (27). No publication bias was observed for any of the metrics (*SI Appendix*, Fig. S2 and Table S1).

Linear mixed-effect meta-regression and model selection. The multiple predictors were analyzed in a mixed-effects meta-regression model by ML estimation to calculate the relative effects on the response of microbial alpha diversity, community dissimilarity, and fungal guilds (42, 43). We did not conduct any regression prediction of the functional rate related to soil organic matter decomposition due to the limited number of available locations including this type of data (i.e., low sample size). The usual mixed-effects meta-regression model is given as:

$$y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_j x_{ij} + u_i + e_i \, i = 1, 2, \cdots, K \tag{9}$$

where x_{ij} is the jth predictor variable in the study i, β_j is the corresponding model coefficient, K is the number of independent studies, u_i is a random effect that is typically assumed to be normally distributed with $u_i \sim N(0, \tau^2)$, and e_i is the within-study error with distribution $e_i \sim N(0, v_i)$ (43).

In the model, we considered five soil properties (i.e., changes or RR in pH, SOC, TN, C:N, and TP to forest conversion), two climatic factors (MAT and AI), forest conversion types (F-Plant, F-Gras, and F-Crop), and biome types (TropF, SubTroF, and TempF) as the predictors. The three forest conversion types were valued with 1 (F-Plant), 2 (F-Gras), and 3 (F-Crop), and the three biomes were valued with 1 (TropF), 2 (SubTroF), and 3 (TempF). Due to high correlation between RR of TN and RR of SOC (Pearson r = 0.708; P < 0.001), we excluded RR of TN from multivariable models to avoid multicollinearity. We included the other RR soil properties in multivariable models. Furthermore, we did not consider nutrient availability as predictors in model because the measuring methods used in sampled literature may not have effectively evaluated those metrics.

We made a model selection based on the corrected Akaike Information Criterion (AIC) to select the most parsimonious multivariate meta-regression model and calculate the relative statistical association of each predictor (i.e., changes in predictors with forest conversion) with microbial alpha diversity, community dissimilarity and fungal guilds (i.e., changes in microbial attributes with forest conversion). The predictors of the most parsimonious model selected by the lowest AIC values are shown in *SI Appendix*, Table S2. The relative importance value of each predictor was determined as the sum of Akaike weights for models that included this predictor, which can be considered as the total support for each predictor across all potential models. The cutoff was set at 0.8 to differentiate between important and nonessential predictors (44). The entire meta-regression and model selection analyses were conducted using glmulti (45) and metafor (46) packages in R (v.4.1.2).

Then, we used a separate linear mixed-effects meta-regression to test the relationships between predictors and soil biodiversity. We selected those relationships between changes in microbial diversity and changes in predictors in response to forest conversion (RR) with a sum of Akaike weights greater than 0.8 (sensu ref. 44) and a significant regression relationship to be displayed using a scatter plot. We also used separate linear mixed-effects regression model to analyze the relationship between the changes in microbial diversity and function associated with changes in organic matter decomposition in response to forest conversion (RR). Finally, we used Spearman correlations to show the directions of the relationship between all the environmental predictors and the responses of microbial diversity and functions to forest conversion (i.e., RR). All the analyses were performed using R (v.4.1.2).

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information. Data associated with this article can be found in ref. 47.

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