Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil bacterial communities

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The Amazon rainforest is the Earth's largest reservoir of plant and animal diversity, and it has been subjected to especially high rates of land use change, primarily to cattle pasture. This conversion has had a strongly negative effect on biological diversity, reducing the number of plant and animal species and homogenizing communities. We report here that microbial biodiversity also responds strongly to conversion of the Amazon rainforest, but in a manner different from plants and animals. Local taxonomic and phylogenetic diversity of soil bacteria increases after conversion, but communities become more similar across space. This homogenization is driven by the loss of forest soil bacteria with restricted ranges (endemics) and results in a net loss of diversity. This study shows homogenization of microbial communities in response to human activities. Given that soil microbes represent the majority of biodiversity in terrestrial ecosystems and are intimately involved in ecosystem functions, we argue that microbial biodiversity loss should be taken into account when assessing the impact of land use change in tropical forests.

deforestation | microorganisms | community similarity | spatial scale | distance decay

Tropical rainforests comprise only 7% of the Earth's land surface, yet they support more than 60% of all known plant and animal species (1). Worldwide, tropical rainforests are facing multiple anthropogenic threats, such as pollution, climate change, and deforestation (2). The Amazon rainforest is the most extensive equatorial forest in the world and represents the largest reservoir of plant and animal species, hosting an estimated one-quarter of all terrestrial species (1). It is under threat from widespread deforestation, primarily for agriculture (3, 4). This ecosystem conversion to agriculture has a substantial impact on the plant and animal biodiversity (3, 4), but the response of microbes is poorly understood, and, in general, little is known regarding the impact of forest conversion to agriculture on soil microbial biodiversity (5). This lack of knowledge is of significant concern because soil microbes, especially bacteria, represent the majority of biodiversity in terrestrial ecosystems and are intimately involved in ecosystem functions, including carbon sequestration and element cycling (6).

Previous studies have shown that biogeochemical cycles mediated by microbial communities, including nitrogen cycling and methane production, are altered by ecosystem conversion in the Amazon rainforest (7–13), and that bacterial community composition in soil can differ between Amazon rainforest and pasture sites (14–16). However, to date, only one study has attempted to determine the response of bacterial diversity to ecosystem conversion in the Amazon (14). This study reported that bacterial diversity was higher in pasture relative to rainforest soils, and the authors suggested that ecosystem conversion in the Amazon rainforest did not "deplete bacterial diversity" (14). This observation is fundamentally different from what is reported for plant and animal diversity, which tends to decrease, both above and belowground, after ecosystem conversion (3, 4, 17). A practical implication of this result is that bacterial biodiversity need not be considered when assessing the impact of large-scale conversion of rainforest to agriculture. However, this study was limited in sampling depth and extent and was focused only on local diversity (alpha diversity in the sense of Whittaker, ref. 18). It thus may have underestimated changes in diversity that occurred over larger geographic scales. Our study was designed to overcome these limitations.

Results

Our study site was Fazenda Nova Vida in Rondônia, Brazil, the most intensively studied ecosystem conversion site in the Amazon region, supported by a large literature regarding the ecosystem responses to conversion at this site (7–13). Soils were sampled along 10-km transects of primary forest and nearby pasture (established in 1987). We used a spatially nested sampling scheme that resulted in 36 soil samples per transect, with intersample distances ranging from centimeters to tens of kilometers (Fig. S1). Bacterial communities from each soil sample were characterized by using barcoded pyrosequencing of the bacterial 16S rRNA gene (15, 19). Sequences were binned into operational taxonomic units (OTUs) by using sequence identity and cut off values of 95 and 97% (19). Community diversity and similarity were calculated by using both taxonomic and phylogenetic measures. Taxonomic similarity was calculated as the proportion of shared OTUs, whereas phylogenetic similarity was calculated as the proportion of shared phylogenetic branch lengths, between two communities.

We estimated local (alpha) diversity (18) as the average richness across all soil samples from a given land use type (forest or pasture). Differentiation (beta) diversity (18) was estimated as both turnover and variation (20). Turnover (estimated as the decay of community similarity with distance) was calculated by determining the slope of the relationship between geographic distance and community similarity for each land use type (20, 21). Variation was estimated as the average pairwise community similarity within each land use type (20).

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We observed that bacterial communities from pasture soils were significantly different from those of forest soils in both taxonomic and phylogenetic composition [analysis of similarity (ANOSIM): $R = 0.555$, $P < 0.001$ for taxonomic, $R = 0.442$, $P < 0.001$ for phylogenetic; Fig. 1]. These differences were evident at both the phylum level (Fig. 1*A*) and the OTU level (Fig. 1 *B* and *C*). The largest proportional decrease in response to conversion was by the phylum *Acidobacteria*, which decreased from an average of 21.1% [±0.05; 95% confidence interval (CI)] of the OTUs identified in the forest to 13.4% (±0.08; 95% CI) of those in the pasture, followed by the phyla *Nitrospirae* and *Gemmatimonadetes*. The largest proportional increase in response to conversion was by the phylum *Firmicutes*, which increased from 2.2% (±0.02; 95% CI) in the forest samples to 12.6% (±0.07; 95% CI) in the pasture, followed by slight increases for *Actinobacteria* and *Chloroflexi*.

Forest and pasture soils also differed in environmental characteristics; for example, forest soils had significantly lower pH, lower total carbon, and higher aluminum concentrations than pasture soils (Table S1). When performing environmental fitting of 12 soil variables onto the nonmetric multidimensional ordination plot (Fig. S2), forest microbial communities were associated with lower pH values and increases in both aluminum concentration and saturation, whereas pasture communities were linked to increases in carbon, nitrogen, and magnesium concentrations.

Bacterial communities from pasture soils were significantly higher in alpha diversity than those of forest soils (Fig. 2). This result was true for both taxonomic richness ($t = -3.63$, $P = 0.001$, df = 1, 64) and phylogenetic diversity ($t = -5.98$, $P < 0.001$, df = 1, 64). In contrast, beta diversity was significantly lower in pasture soils: Bacterial communities were significantly more similar in composition and had significantly lower turnover across space. This result was true of both taxonomic and phylogenetic measures of similarity (taxonomic: $t = 14.3$, $P < 0.001$, df = 1, 434; phylogenetic: $t = 6.62$, $P < 0.001$, df = 1, 434; Fig. 3) and both taxonomic and phylogenetic measures of turnover (analysis of covariance: $F = 32.0$, $P < 0.001$ for taxonomic; $F = 49.8$, $P < 0.001$ for phylogenetic; Fig. 4).

Discussion

The uncoupling of alpha and beta diversity after ecosystem conversion that we observed is not commonly observed for plants and animals in the Amazon, where conversion usually results in decreases in both (3). However, in general, alpha diversity is not always coupled to beta diversity (22), and there are reports of plant and animal communities that respond to anthropogenic disturbance with an increase in alpha diversity and a decrease in beta diversity (23, 24). Such systems tend to have relatively low rates of productivity that increase after ecosystem conversion (24). Our site is consistent with this observation; despite high aboveground primary productivity, belowground primary productivity is low, and it increases dramatically after the establishment of pasture (16, 25). This effect is true for microbial belowground productivity (defined as turnover of microbial biomass) as well (16, 25). This difference in starting productivity may explain why bacteria respond differently than plants and animals to ecosystem conversion in our system.

Our results show that bacterial community composition was significantly altered by the forest-to-pasture conversion. Cultivated members of the phylum *Acidobacteria* are known oligotrophs, responding negatively to incremental increases in carbon and pH (26), which may explain the strong decrease in the proportion of sequences detected from this phylum after conversion. The majority of the members representing the phylum *Firmicutes* have notable resistance to desiccation and extremes of environmental variation (27). These microorganisms are known to thrive in environments where carbon is highly available and soil surface temperatures vary throughout the day (such as the pastures sampled in our study), which may explain the substantial increase in the proportion of sequences detected from this phylum after conversion.

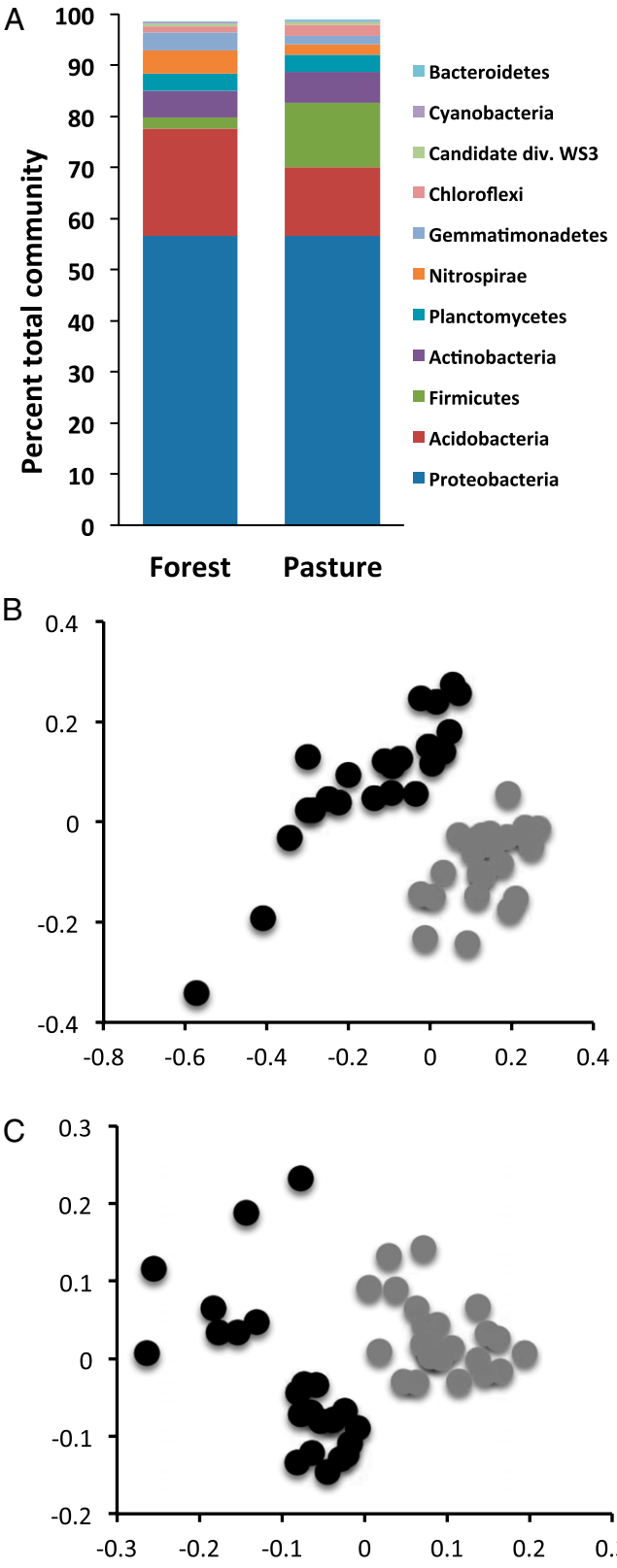

Fig. 1. Bacterial community composition of pasture and forest soil samples. (*A*) Distribution of 16S rRNA sequences across bacterial phyla in forest and pasture. (*B*) Nonmetric multidimensional scaling plot of taxonomic similarity (Bray–Curtis). (*C*) Nonmetric multidimensional scaling plot of phylogenetic similarity (FastUnifrac). Gray circles, pasture samples; black circles, forest samples.

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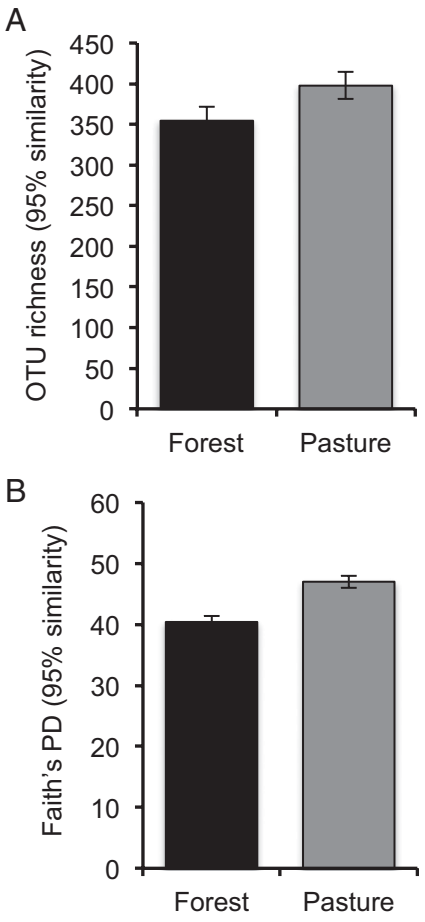

Fig. 2. Response of local diversity to ecosystem conversion. (*A*) Estimated taxonomic richness (abundance-based coverage estimator), (*B*) PD. Means ($n = 33$) are depicted, ±95% CI.

Our results have several important implications. The decrease in beta diversity in response to ecosystem conversion is an indication of biotic homogenization (28), the process by which the similarity of communities increases over time and/or space (22). Biotic homogenization of plant and animal communities is a common result of ecosystem conversion, but it is unique for microorganisms. Biotic homogenization can occur through the loss of taxa with restricted geographic ranges ("endemic" taxa), the invasion of taxa with broad ranges, and/or an increase in the ranges of existing species (e.g., through the removal of dispersal barriers; ref. 22). We asked which of these mechanisms were at play in our system by comparing the distribution across soil cores of bacterial taxa found only in the forest, only in the pasture, and those found in both habitats. There is no evidence for invasion by broadly distributed taxa. However, there is evidence for both an increase in the ranges of existing taxa (taxa found in both habitats were found in significantly fewer cores in the forest than in the pasture; $t = -23.7$, $P < 0.001$, df = 3586; Fig. 5) and loss of forest endemics (taxa unique to the forest occur in significantly fewer cores than other taxa; $t = -34.7$, $P < 0.001$, df = 3929; Fig. 5). The loss of endemic taxa is of particular concern because, by definition, such taxa have unique ecological requirements and, thus, tend to have unique traits and trait combinations (29). Increased phylogenetic similarity in the pasture (Figs. 2 and 3) suggests that the diversity of traits that are phylogenetically conserved will decline after conversion. Such trait homogenization is predicted to alter ecosystem function and reduce ecosystem resilience to disturbance (28, 29).

Another implication of our results is that biotic homogenization could counterbalance increases in local diversity due to ecosystem conversion, resulting in a net loss of diversity. There is evidence that this diversity loss is occurring in our system. Taxa accumulate with increasing sampling effort more rapidly in the forest than in the pasture (Fig. S3). The result is that at relatively low levels of sampling, forests appear to have fewer taxa on average than pastures, but as sampling effort increases, the forest eventually surpasses the pasture in taxonomic richness. The difference we observed across all of our samples likely represents a minimum loss of diversity due to ecosystem conversion, because the accumulation curves are not yet approaching asymptotes. More extensive sampling would be necessary to reveal the true loss of diversity. However, given the very broad taxon definitions we used (i.e., 95% and 97% sequence identity), even this minimum difference represents the loss of a substantial amount of genetic variation after ecosystem conversion.

The long-term impact of this loss of diversity is not yet known. In particular, it is not known whether the changes in diversity we observed are reversible after agricultural abandonment. Amazon forest sites that have been converted to pasture and subsequently abandoned have been observed to reestablish forest, although this forest is commonly of lower plant diversity than forest with no history of conversion (30). Whether bacterial diversity will

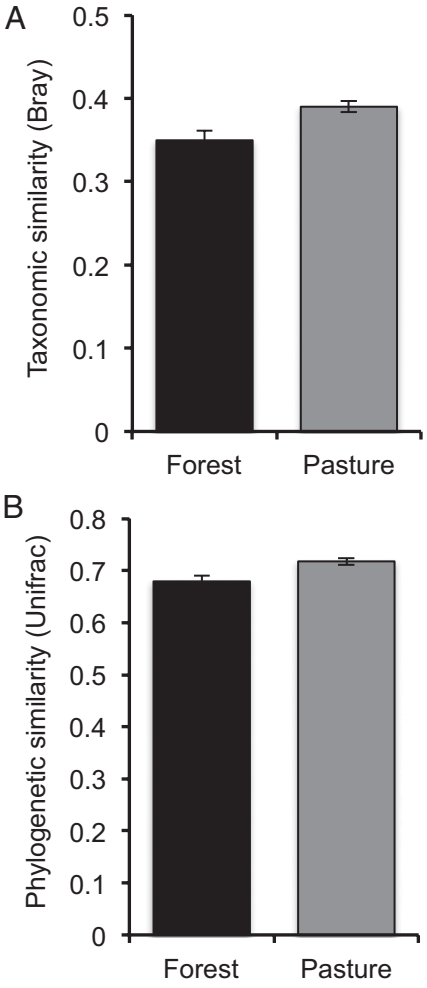

Fig. 3. Response of community similarity to ecosystem conversion. (*A*) Average taxonomic similarity (Bray–Curtis), (*B*) Average phylogenetic similarity (FastUnifrac). Means ($n = 435$) are depicted, ±95% CI.

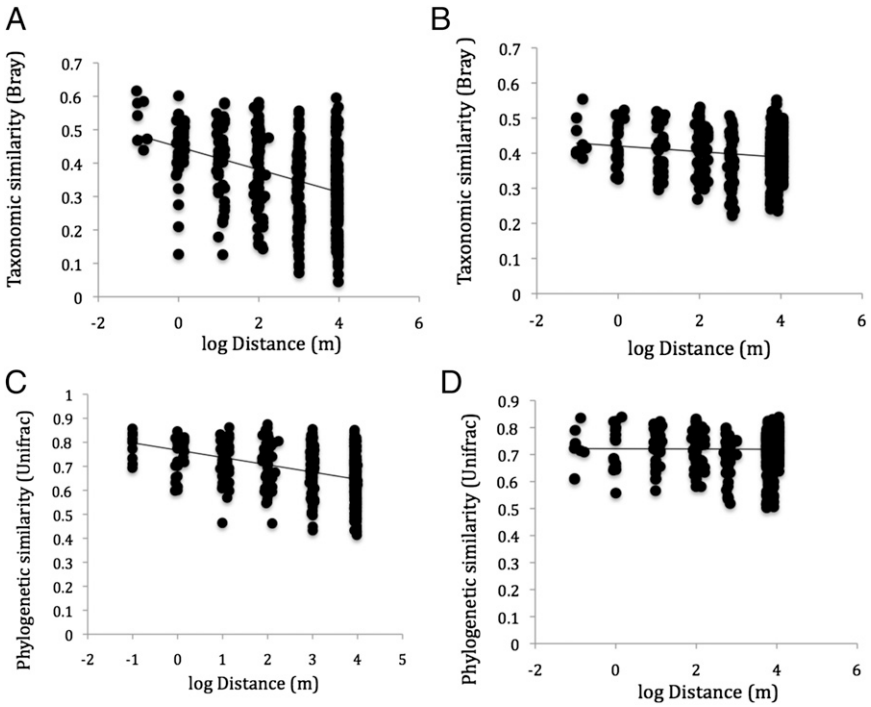

Fig. 4. Response of community turnover to ecosystem conversion. (*A*) Decay of taxonomic similarity (Bray–Curtis) with geographic distance in forest. (*B*) Decay of taxonomic similarity (Bray–Curtis) with geographic distance in pasture. (*C*) Decay of phylogenetic similarity (FastUnifrac) with geographic distance in forest. (*D*) Decay of phylogenetic similarity (FastUnifrac) with geographic distance in pasture.

completely recover from ecosystem conversion will depend in part on whether the taxa lost due to conversion are truly locally extinct or whether they are present in pasture sites but of such low abundance that they are undetectable in our study. We used high-throughput, next-generation sequencing to generate a comprehensive sampling of soil bacteria at our site. However, this sampling is not exhaustive (although, it should be pointed out, neither are most studies of plant diversity in the Amazon). Regardless, we observed at a minimum a significant reduction in the abundance of forest endemics and the traits they possess, as well as significant homogenization of those taxa we did detect, in response to ecosystem conversion.

Conclusions

For at least the past 40 y, there has been great concern that the conversion of the Amazon rainforest into agricultural systems would result in the loss of animal and plant diversity (22). We have shown that microbial diversity is also altered by such environmental change. Furthermore, the specific response we observed—an increase in alpha diversity and a decrease in beta diversity after environmental change—has been suggested as an "early warning signal" for future biodiversity loss (23). It is not yet clear exactly how microbial diversity is related to ecosystem function (31), nor has it been definitively established for plant or animal diversity (e.g., ref. 32). However, given the role microbes play as mediators of many important ecosystem functions (6), the loss of microbial diversity in response to ecosystem conversion should be of concern.

Materials and Methods

Sample Site. Our study was performed at the Amazon Rainforest Microbial Observatory (ARMO) site, established in 2009 and located at the coordinates 10°10′5″ S and 62°49′27″ W. It was chosen as a model site to represent the current expansive agricultural development occurring in the Amazon region. This site is located within Rondônia State, which has the highest percentage of forest loss (28.5%) of any state in the Brazilian Amazon. Common practice for this agricultural frontier is selective logging of timber trees, followed by cutting and burning of the remaining vegetation. Pastures for cattle production are then established by aerial seeding of fast growing nonnative grasses. Weeds in the pastures may be controlled by occasional burning. No herbicides, tillage, or chemical fertilizers are commonly used. When the soil becomes unproductive and is abandoned, secondary forest develops, which is commonly of lower plant diversity than the original forest (30).

The site selected for ARMO is the Fazenda Nova Vida, a research station that is part of the Large Scale Biosphere-Atmosphere Experiment in Amazonia (www.lbaeco.org/lbaeco). The general plant community composition at Fazenda Nova Vida has been described (33). In brief, the pastures are dominated by the grasses *Urochloa brizantha*, *Urochloa decumbens* (formerly the genus *Brachiaria*), or *Panicum maximum* (or a mix of two of the three). The primary forest is a typical wet Terra Firme forest of the "Open Forest with Palms" variety (30). Identified species in the primary forest include *Orbignya phalerata, Tabebuia* spp., *Erisma uncinatum,* and *Vismia guianensis*, although the majority of species are unidentified. The soil at our sites is a red-yellow podzolic latosol (Kandiudult), sandy loam in texture, and has been described in detail (34).

Sample Design. We established plots within primary forest and pasture. At each site, a nested sampling scheme has been established, centered on a 100-m^2 quadrat, with 10-m^2, 1-m^2, 0.1-m^2, and 0.01-m^2 quadrats nested within, for a total of 12 sampling points per 100-m^2 quadrat (Fig. S1). This spatially explicit sampling scheme allows the assessment of not only richness at each sample site (alpha diversity) and across each land use type (gamma diversity), but also turnover in community composition across sites, one of the approaches used to estimate beta diversity (20).

Our samples were taken at the end of the rainy season (April 13–17, 2009). Soil was sampled to 10 cm (after removing the litter layer) by using standard coring methods, homogenized and subdivided. Soil for molecular analysis was stored at −20 °C, and soil for other applications (e.g., soil physicochemical properties) was stored at 4 °C before analysis.

Soil Chemical Analysis. Soil samples were air dried and sieved to a 100 mesh for total C and N determination through dry combustion on a LECO CN elemental analyzer at the Centro de Energia Nuclear na Agricultura, University of Sao Paulo, Brazil. The soil attributes pH, P, S, K, Ca, Mg, Al^{+}, and base saturation (%V) were analyzed at the Laboratorio de Fertilidade do Solo, Department of Soil Sciences, University of Sao Paulo.

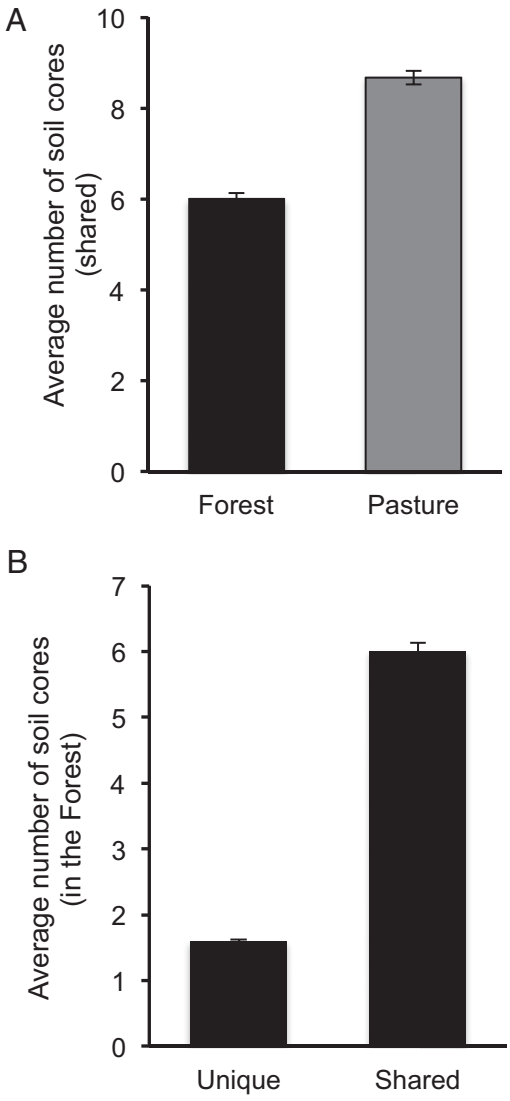

Fig. 5. Distribution of bacterial OTUs across soil cores. (*A*) Distribution in forest and pasture of OTUs shared between forest and pasture. (*B*) Distribution in forest of OTUs unique to forest and OTUs shared between forest and pasture.

DNA Extraction, PCR, and DNA Sequencing. Soil DNA was extracted in triplicate from each sample with the PowerSoil DNA Isolation kit (MoBio Laboratories) by using manufacturer's instructions. DNA extractions from the same soil sample were combined, quantified with the Nanodrop ND-1000 spectrophotometer, and stored at −20 °C. DNA extractions for both treatments had an average of 11.4 ng/μL (±2.3 SD) and 9.8 ng/μL (±1.9 SD) for forest and pasture samples, respectively. All samples were spectrophotometrically quantified with A_{260}/A_{280} ratio averages of 1.78 and 1.84 for forest and pasture, respectively. Primers 577F (5′-AYTGGGYDTAAAGNG-3′) and 926R (5′-CCGTCAATTCMTTTRAGT-3′) targeting the region V4 of the 16S rRNA gene were used for PCR, because sequences in that region provide comprehensive coverage (35) and among the highest taxonomical accuracy (36, 37). Primers were designed with eight-base barcodes and 454 pyrosequencing adapters (Integrated DNA Technology). Amplification reactions were performed in 50-μL volume containing 1× buffer, 0.2 μM of each primer, 1.8 mM $MgCl_2$, 200 μM deoxynucleoside triphosphates, 300 ng/μL BSA, 10 ng of template, and 1 μL of the FastStart High Fidelity PCR System enzyme (Roche Applied Sciences). Amplification was initiated with 3 min at 95 °C, followed by 30 cycles of denaturation at 94 °C for 45 s, primer annealing at 57 °C for 45 s, extension at 72 °C for 1 min, and final extension for 4 min. Reactions, performed in triplicate, were combined and purified by using gel electrophoresis followed by the QIAquick gel extraction kit and the Qiagen PCR purification kit.

High-throughput sequencing was performed with the 454 GS FLX Sequencer (454 Life Sciences) at the Michigan State University Research Technology Support Facility. We used the recommendations by Huse et al. (38) and removed reads that contain one or more N's, reads where the lengths lied outside of the main distribution, and those with inexact matches to the primer.

Sequence Analysis. All sequence processing was done by using the bioinformatics platform mothur (39). Sequences were discarded if they contained ambiguous base calls, were less than 300 nt or more than 400 nt in length, or if they contained more than 20 homopolymers. Sequences that passed these quality filters were aligned by using the Ribosomal Database Project (RDP; http://rdp.cme.msu.edu) reference alignment. Pairwise distances between sequences were calculated by using the furthest neighbor algorithm, and OTUs were delineated at both 95% and 97% sequence similarity. The two similarity cutoffs gave qualitatively similar results. Results using the 95% cutoff are presented because this cutoff minimizes the chance of artifactual OTU assignment due to sequencing error. OTUs were assigned to taxonomic groups by using a randomly selected representative sequence with the classifier platform within the RDP.

Data Analysis. All analyses were conducted by using the package picante (40) with the statistical platform R. Because of unequal numbers of sequences among soil cores, samples were rarefied to 1,000 sequences, and samples with less than 1,000 sequences were not included in the analyses (only five samples met this criterion and were excluded). Rarefaction was repeated 30 times, and each subsequent analysis was based on the means of the 30 random trials. Phylogenetic analyses were based on a tree built with representative OTUs by using the program FastTree2 (41).

Taxonomic alpha diversity was calculated as estimated richness by using the abundance-based coverage estimator (ACE) (42) and compared by using a Student's *t* test. Phylogenetic diversity was calculated as Faith's phylogenetic diversity (PD) (43).

Taxonomic community similarity was calculated by using the Bray–Curtis index. Phylogenetic community similarity was calculated by using FastUnifrac (44). Taxonomic and phylogenetic community composition was compared between forest and pasture sites by using ANOSIM (45). The pairwise geographic distances between cores were calculated based on geographic coordinates and physical measurements. Community turnover (i.e., the distance decay of similarity) was determined by regressing the pairwise community similarity against the pairwise geographic distance using linear regression.

Gamma diversity was calculated by using species accumulation curves with random sampling among cores within sites and richness estimated by using the ACE measure. Accumulation of phylogenetic diversity was calculated by randomly sampling the PD across soil cores within sites.

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1. Dirzo R, Raven PH (2003) Global state of biodiversity and loss. *Annu Rev Environ Resour* 28:137–167.
2. Laurance WF, Peres CA (2006) *Emerging Threats to Tropical Forests* (Univ Chicago Press, Chicago).
3. Bierregaard RO, Gascon C, Lovejoy TE, Mesquita R (2001) *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest* (Yale Univ Press, New Haven, CT).
4. Soares-Filho BS, et al. (2009) Modeling conservation in the Amazon basin. *Nature* 440(7083):520–523.
5. Verchot LV (2010) *Soil Biology and Agriculture in the Tropics*, ed Dion P (Springer, Berlin), pp 45–64.
6. Madsen EL (2011) Microorganisms and their roles in fundamental biogeochemical cycles. *Curr Opin Biotechnol* 22(3):456–464.
7. Herpin U, et al. (2002) Biogeochemical dynamics following land use change from forest to pasture in a humid tropical area (Rondônia, Brazil): A multi-element approach by means of XRF-spectroscopy. *Sci Total Environ* 286(1-3):97–109.
8. Moraes JFL, Volkoff B, Cerri CC, Bernoux M (1996) Soil properties under Amazon forest change due to pasture installation in Rondonia, Brazil. *Geoderma* 70(1):63–81.

9. Neill C, et al. (1997) Net nitrogen mineralization and net nitrification rates in soils following deforestation for pasture across the southwestern Brazilian Amazon Basin landscape. *Oecologia* 110(2):243–252.
10. Neill C, Piccolo MC, Melillo JM, Steudler JA, Cerri CC (1999) Nitrogen dynamics in Amazon forest and pasture soils measured by N-15 pool dilution. *Soil Biol Biochem* 31(4):567–572.
11. Neill C, et al. (1995) Nitrogen dynamics in soils of forests and active pastures in the western Brazilian Amazon Basin. *Soil Biol Biochem* 27(9):1167–1175.
12. Reiners WA, Bouwman AF, Parsons WF, Keller M (1994) Tropical rainforest conversion to pasture - changes in vegetation and soil properties. *Ecol Appl* 4(2):363–377.
13. Fernandes SAP, Bernoux M, Cerri CC, Feigl BJ, Piccolo MC (2002) Seasonal variation of soil chemical properties and CO2 and CH4 fluxes in unfertilized and P-fertilized pastures in an Ultisol of the Brazilian Amazon. *Geoderma* 107(3):227–241.
14. Jesus ED, Marsh TL, Tiedje JM, Moreira FMD (2009) Changes in land use alter the structure of bacterial communities in Western Amazon soils. *ISME J* 3(9):1004–1011.
15. Borneman J, Triplett EW (1997) Molecular microbial diversity in soils from eastern Amazonia: Evidence for unusual microorganisms and microbial population shifts associated with deforestation. *Appl Environ Microbiol* 63(7):2647–2653.
16. Cenciani K, Lambais MR, Cerri CC, de Azevedo LCB, Feigl BJ (2009) Bacteria diversity and microbial biomass in forest, pasture and fallow soils in the southwestern Amazon Basin. *Rev Bras Cienc Solo* 33(4):907–916.
17. Lavelle P, Pashanasi B (1989) Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiologia (Jena)* 33(5):283–291.
18. Whittaker RH (1975) *Communities and Ecosystems* (Macmillan Publishers, New York).
19. Roesch LF, et al. (2007) Pyrosequencing enumerates and contrasts soil microbial diversity. *ISME J* 1(4):283–290.
20. Anderson MJ, et al. (2011) Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecol Lett* 14(1):19–28.
21. Soininen J, McDonald R, Hillebrand H (2007) The distance decay of similarity in ecological communities. *Ecography* 30(1):3–12.
22. Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *Am Nat* 162(4):442–460.
23. Hewitt J, Thrush S, Lohrer A, Townsend M (2010) A latent threat to biodiversity: Consequences of small-scale heterogeneity loss. *Bio Cons* 19(5):1315–1323.
24. Smart SM, et al. (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proc Biol Sci* 273(1601):2659–2665.
25. Cerri CEP, et al. (2004) Modeling changes in soil organic matter in Amazon forest to pasture conversion with the Century model. *Glob Change Biol* 10(5):815–832.
26. Eichorst SA, Breznak JA, Schmidt TM (2007) Isolation and characterization of soil bacteria that define Terriglobus gen. nov., in the phylum Acidobacteria. *Appl Environ Microbiol* 73(8):2708–2717.
27. Battistuzzi FU, Hedges SB (2009) A major clade of prokaryotes with ancient adaptations to life on land. *Mol Biol Evol* 26(2):335–343.
28. Olden JD, Leroy Poff N, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol Evol* 19(1):18–24.
29. McKinney ML, Lockwood JL (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14(11):450–453.
30. Pires JM, Prance GT (1985) *Key Environments: Amazônia*, eds Prance GT, Lovejoy TE (Pergamon, Oxford), pp 109–145.
31. Langenheder S, Bulling MT, Solan M, Prosser JI (2010) Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity. *PLoS ONE* 5(5): e10834.
32. Srivastava D, Vellend M (2005) Biodiversity-Ecosystem function research: Is it relevant to conservation? *Annu Rev Ecol Evol Syst* 36:267–294.
33. Feigl B, et al. (2006) Biological survey of a low-productivity pasture in Rondônia state, Brazil. *Agriculture* 35(6):199–208.
34. Neill C, et al. (1997) Soil carbon and nitrogen stocks following forest clearing for pasture in the southwestern Brazilian Amazon. *Ecol Appl* 7(4):1216–1225.
35. Sul WJ, et al. (2011) Bacterial community comparisons by taxonomy-supervised analysis independent of sequence alignment and clustering. *Proc Natl Acad Sci USA* 108(35):14637–14642.
36. Wang Q, Garrity GM, Tiedje JM, Cole JR (2007) Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl Environ Microbiol* 73(16):5261–5267.
37. Nossa CW, et al. (2010) Design of 16S rRNA gene primers for 454 pyrosequencing of the human foregut microbiome. *World J Gastroenterol* 16(33):4135–4144.
38. Huse SM, Huber JA, Morrison HG, Sogin ML, Welch DM (2007) Accuracy and quality of massively parallel DNA pyrosequencing. *Genome Biol* 8(7):R143.
39. Schloss PD, et al. (2009) Introducing mothur: Open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl Environ Microbiol* 75(23):7537–7541.
40. Kembel SW, et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26(11):1463–1464.
41. Price MN, Dehal PS, Arkin AP (2010) FastTree 2—approximately maximum-likelihood trees for large alignments. *PLoS ONE* 5(3):e9490.
42. Chao A, Lee SM (1992) Estimating the number of classes via sample coverage. *J Am Stat Assoc* 87(417):210–217.
43. Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61(1):1–10.
44. Lozupone C, Hamady M, Knight R (2010) Fast UniFrac: Facilitating high-throughput phylogenetic analyses of microbial communities including analysis of pyrosequencing and PhyloChip data. *ISME J* 4(1):17–27.
45. Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. *Aust J Ecol* 18(1):117–143.