Impacts of land-use change on soil microbial communities and their function in the Amazon Rainforest

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Advances in Agronomy
ISSN 0065-2113
https://doi.org/10.1016/bs.agron.2022.04.001

Abstract

The Amazon Rainforest is a global diversity hotspot that has experienced a significant level of deforestation over the past half century, primarily for the establishment of cattle pasture. Characterizing the impact of this large-scale ecosystem conversion on the composition and activity of the soil microbial community is crucial for understanding potentially consequential shifts in nutrient and greenhouse gas cycling, as well as adding to the body of knowledge concerning how tropical ecosystems respond to human disturbance. Research to date has shown that locally, communities of soil microorganisms tend to become more diverse upon conversion of forest to pasture. However, these communities undergo taxonomic homogenization at landscape-level spatial scales, mirroring the homogenization of plant communities across pastures. Microbial community structure is distinct between forest and pasture soil communities across several studies, and specific taxa, such as Firmicutes and Acidobacteria, show consistent association with pasture and forest soils, respectively. In addition, shifts in microbial community functions with pasture conversion have relevant impacts on both carbon and nitrogen cycling at the ecosystem scale: the abundance and diversity of methane-cycling prokaryotes shifts in conjunction with increased methane flux in pastures. Further, quantitation and community profiling of free-living nitrogen fixers has demonstrated that this functional group is favored in pastures and suggests that asymbiotic N_2 fixation may be a significantly augmented process. While human-driven deforestation is continuing, a large percentage of once-converted pastures are undergoing the process of secondary forest succession. Assessment of microbial communities in secondary forests compared to primary forests and pastures suggests convergence toward a recovery of functionality and community composition with reforestation.

Abbreviations

ANF	associative/asymbiotic nitrogen fixation
AOA	ammonia oxidizing archaea
AOB	ammonia oxidizing bacteria
ARMO	amazon rainforest microbial observatory
ASV	amplicon sequence variant
BLA	Brazilian Legal Amazon
CEC	cation exchange capacity
MAG	metagenome-assembled genome
MB	microbial biomass
SNF	symbiotic nitrogen fixation
T-RFLP	terminal restriction fragment length polymorphism

1. Introduction: The Amazon is an ecosystem of global importance

The Amazon Basin contains the largest tropical forest on Earth, covering a cumulative area of 6.3 million square kilometers across eight different

countries (plus the Territory of Guiana) in South America, although over two-thirds of its total area is contained within Brazil's borders (Butler, 2020; Hansen et al., 2020). The basin plays a major role in the planet's biosphere, supplying one fifth of the total freshwater flow to the oceans, controlling regional climate parameters, including temperature and precipitation, and regulating the exchange of atmospheric gases (Coe et al., 2017; Davidson et al., 2012). The Amazon Rainforest also contains a disproportionately high number of plants and animals in comparison to any other ecosystem on the planet (i.e., a hotspot), potentially housing 25% of all terrestrial species, including approximately 16,000 tree and 1300 bird species (Barlow et al., 2018; Butler, 2020; Dion, 2010; Gaston, 2000; Oliviera and ter Steege, 2013).

Total rates of deforestation in the Amazon are difficult to assess due to differential coverage of satellite data across the region over the past several decades. Likely the most comprehensive data source available, Brazil's National Institute for Space Research recorded approximately 45,700 km^2 of deforestation between 1988 and 2020 using satellite imagery (Fig. 1A). Another 345,000 km^2 is estimated to have been lost between 1970 and 1987, amounting to a cumulative projection of 18–20% of Brazil's historic coverage (INPE, 2020). During the first half of the 1970s, the widespread development of highways was likely an important catalyst for increased rates of deforestation. These highways afforded new access to the Amazon and created a feedback loop of speculative buying, land clearing, and subsequent inflation of value, driving further speculative buying (Fearnside, 1987). The progression of deforestation throughout the Amazon Rainforest Biome has left small, disconnected fragments of primary forest across a disturbed landscape (Lovejoy et al., 1986). Annual rates of loss peaked in the early 2000s before falling dramatically in 2005, though rates have been on the rise again since 2015, particularly within the Brazilian Legal Amazon (BLA; Fig. 1A).

By far the most common cause of forest clearing in the Amazon Basin is for the establishment of cattle pasture, accounting for approximately 68% of land-use change-driven clearing between 2000 and 2013 in the BLA (Tyukavina et al., 2017). The establishment of small- and large-scale agriculture accounted for 13% and 11% of forest clearing over this same period, respectively (Fig. 1B). The remaining <8% of clearing resulted from activities including logging, construction, and mining (Tyukavina et al., 2017). The prevalence of pasture across the Amazon has heavily influenced the focus of research into the environmental and ecological implications of this conversion type, and consequently, forest-to-pasture comparative studies in the BLA will be the main focus of this chapter.

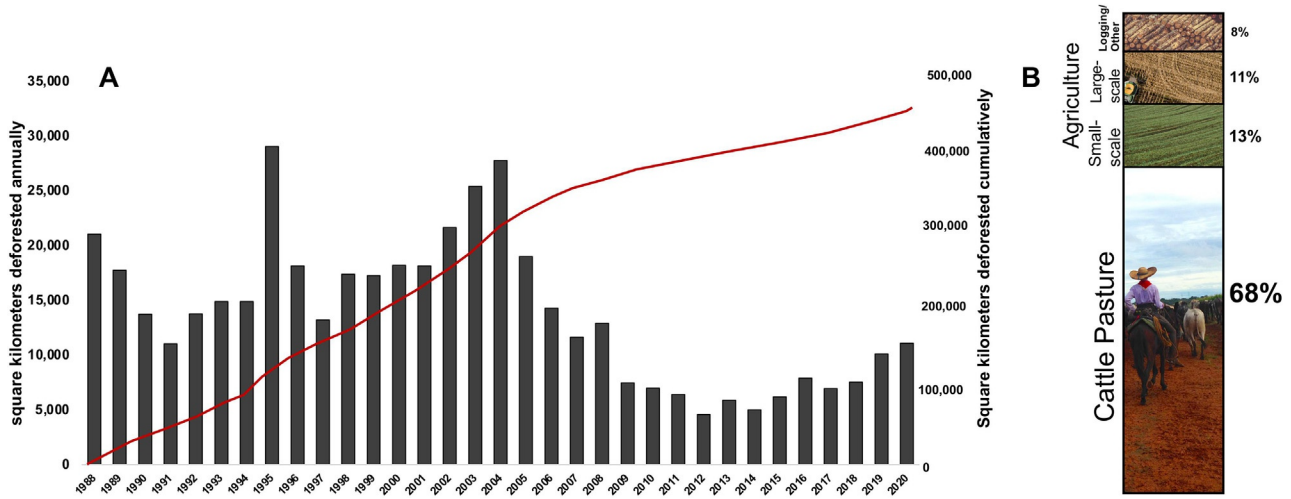

Fig. 1 Patterns of deforestation in the Brazilian Legal Amazon from 1988 to 2020. (A) Annual rates of deforestation in square kilometers (dark gray bars, left axis) overlaid with cumulative forest loss (red line, right axis). Data obtained from Brazil's National Institute for Space Research (INPE) DETER satellite imagery. (B) Causes of deforestation, shown as relative percent of total, normalized to exclude general "fire" category using Tyukavina et al. (2017) data. Large-scale agriculture includes agro-industrial crop production such as soy as well as plantations, whereas small-scale agriculture refers to both subsistence farming and small commercial operations. The "other" category may include mining, construction of roads and urban areas, dams, and more. *Photo used for "pasture" segment courtesy Jorge Rodrigues. Logging, small- and large-scale agriculture photos obtained from Unsplash.com.*

Pasture conversion across the region typically begins with selective logging to remove valuable timber, followed by clear cutting and burning of the remaining vegetation. To establish a pasture, sites are aerially reseeded with fast-growing African perennial bunchgrass species (Mueller et al., 2014; Navarrete et al., 2015a). Dominant species include *Urochloa brizantha*, *Urochloa decumbens*, *Brachiaria humidicola*, and *Panicum maximum*, of which *U. brizantha* and *U. decumbens* are estimated to cover approximately 75% of total pasture area (Jank et al., 2014; Nogueira, 2012). The use of fertilizers on pasture is atypical throughout much of the Amazon due to cost limitations (Jank et al., 2014; Mueller et al., 2014); therefore, productivity of grasses may be very vulnerable to overgrazing. The carrying capacity of the pastures is typically considered to be 1.1 ha per cattle head with improved cultivars of *U. brizantha*, but large variation in seasonality and rotational periods across managed ranches may not reflect the reality of this estimate (Jank et al., 2014; Pedreira et al., 2015).

The process of forest removal has a calculated net efflux of 325 Tg carbon (C) per year through biomass burning and degradation of remaining forest margins (Baccini et al., 2017). Data further shows a curtailing of the South American monsoonal circulation in response to deforestation (Boers et al., 2017). The reduction in condensational latent heat over once-forested areas results in lower inflow of atmospheric moisture from the Atlantic Ocean (Boers et al., 2017; Ciemer et al., 2020), resulting in conditions such as recurrent drought that accelerate tree mortality (Phillips et al., 2009). Consequently, future deforestation may approach a dangerous tipping point where forest-derived latent heat is insufficient to maintain the Atlantic moisture feedback (Boers et al., 2017), leading some to suggest the potential savannization of the entire ecosystem (Silvério et al., 2013). It is crucial, therefore, to understand current and future biological response to Amazon land-use change.

In terms of landscape-scale ecological response, perhaps the most conspicuous consequence of forest conversion in the Amazon is the loss of highly diverse and endemic floral and faunal communities, and replacement with a small number of forage grasses, crops, and cattle (Ferraz et al., 2003). Unfortunately, some undesirable species have thrived; populations of *Anopheles darlingi*, a mosquito vector that transmits malaria, has gained habitat range due to the process of forest clearing removing physical barriers to their dispersal. This has ultimately increased the risk of malaria infection up to 300-fold across the region (Vittor et al., 2006).

A microcosm of the global biosphere with a somewhat ambiguous response to anthropogenic disturbance is the soil microbial community. Soil is known to harbor the highest known taxonomic and functional diversity across different environments, but its composition is largely undescribed (Bahram et al., 2021; Torsvik and Øvreås, 2002). The focus of this chapter will be to review what is currently known about the effects of human-induced land-use change in the Amazon Rainforest on soil microbial communities in terms of diversity and composition, as well as in relation to important microbially-mediated biogeochemical cycles. Also to be discussed are the specific factors of land-use conversion by fire and the recovery of secondary forests from abandoned pasture, which at present comprises a significant portion of the Amazon Rainforest. Current limitations in knowledge and considerations for interpreting data in light of regional differences, such as climate and endemic soil conditions, will be highlighted. In this chapter, we aim to convey the potential importance of expanding our understanding of soil microbial response to large-scale land-use change and will provide insight as to future directions for research efforts.

2. Why do microbes matter?

At first thought, considering the impact of land-use disturbance on soil microbial communities may seem somewhat abstruse, given that their species diversity and environmental activity is unseen to the human eye. Yet, closer examination reveals their relevance as major drivers of a myriad of crucial biogeochemical processes within the soil-plant-atmosphere continuum. Plants interact intimately with microbial community constituents, including archaea, bacteria, and fungi at-or-near their root surfaces (i.e., the rhizosphere). In many cases, plants rely on microbes for nutrient acquisition. Microorganisms collectively produce a complex suite of extracellular enzymes, aide in extension of soil exploration via hyphal networks, and can directly provide plants with nitrogen (N) through root nodule structures in exchange for carbon-rich root exudates (Brzostek et al., 2012; Desbrosses and Stougaard, 2011; Huang et al., 2014; Linderman, 1991). These relationships are important considerations for understanding or predicting plant community succession or overall ecosystem function and sustainability following land-use change.

In addition to their direct relationships with plants, soil microbial communities mediate biogeochemical cycles relevant to greenhouse gas

emissions and climate change. Heterotrophic soil microorganisms are primary agents of soil organic matter decomposition, typically accounting for the bulk of CO_2 released from soils (Yuste et al., 2011). Evidence suggests that substrate affinity competition between various microbial functional groups controls the rate of C mineralization (Fontaine et al., 2004; Fontaine and Barot, 2005). Therefore, shifts in organic matter composition or soil conditions such as pH, temperature, moisture, and bulk density, with land-use change may impact decomposition rates and C use efficiency by altering the composition and interactions of the microbial community. This in turn may influence CO_2 emissions and long-term soil C storage (Öquist et al., 2016).

At present, our collective understanding of the relationship between the distribution of organisms within a given soil habitat and their functional importance is limited (Torsvik and Øvreås, 2002). In the context of large-scale anthropogenic land-use change, shifts in soil microbial processes and physiological plasticity could have key consequences in biogeochemical cycles (Mackelprang et al., 2011). Augmenting our understanding of these relationships has the potential to greatly enhance our ability to predict nutrient transformations and improve the representation of microbial processes in nutrient cycling models (Bradford et al., 2016; Treseder et al., 2011). Studies suggest that microbial community features, like composition and diversity, correspond to rates of activity at varying scales (Chen et al., 2019; Delgado-Baquerizo et al., 2016; Peter et al., 2011; Philippot et al., 2013; Strickland et al., 2009; van Elsas et al., 2012); however, more work is needed to understand the functional overlap across community members and how specific biogeochemical processes are impacted by changes in these communities.

The task of linking (1) the impact of land-use disturbance on the soil environment, (2) microbial community parameters including diversity, composition, and abundance, and (3) shifts in the soil functions they mediate, is immense. Attempting to resolve these complex abiotic and biotic relationships relies upon a variety of molecular methods typically targeting specific groups or whole soil communities, paired with activity measurements and relevant biogeochemical parameters. The next section will briefly review the modern methodologies available to researchers in order to characterize soil microbial communities. Additionally, important terms used to define microbial community diversity will be explained. This will serve as a useful pretext in understanding the work being done by researchers to understand the response of soil microbial communities to land-use change throughout the Amazon Rainforest.

3. Characterizing soil microbial communities: Current methodologies and metrics

3.1 Methods to study complex communities

A straightforward, but fairly low-resolution method of gauging microbial community response to disturbance is through bulk biomass measurement, with the underlying assumption that a reduction in biomass corresponds to a negative impact, or vice versa. In soils, such measurements are made through chloroform fumigation and subsequent extraction and quantification of biomass-derived C and N (DeLuca et al., 2019). This can be put into the context of a community-wide activity response by measuring processes, such as respiration (either under ambient conditions or in response to a variety of substrates), in order to infer catabolic diversity or stress response based on C use efficiency (Degens and Harris, 1997; Wardle and Ghani, 1995). These methods do not, however, provide a dimension of genetic differentiation among community members and lack a detailed understanding of microbial diversity.

A comprehensive means of understanding the physiology and genetics of a microorganism is through culturing. When studying communities as complex as those found in soil, though, culturing is a rather impractical way of gauging diversity or microbial response to environmental change. Only a handful of microorganisms relative to global diversity have been successfully cultured (Handelsman, 2004; Overmann et al., 2017; Schloss and Handelsman, 2004), and even just a gram of soil is likely to contain billions of cells and thousands of distinct organisms (Trevors, 2010). Methods like phospholipid fatty-acid analysis (PLFA), terminal restriction fragment length polymorphism (T-RFLP), and denaturing gradient gel electrophoresis (DGGE) are not dependent on culturing and allow limited characterization of community profiles, but lack the sensitivity of molecular-based approaches and risk misinterpretation of community composition (Dickie et al., 2002; Nakatsu et al., 2000; Schoug et al., 2008).

The most common modern method employed to study microbial communities is the extraction of total soil community DNA and molecular amplification by polymerase chain reaction (PCR). A simple approach to measuring abundance of microbial groups is through quantitative PCR, which allows calculation of gene copy number using a fluorescently tagged DNA polymerase (Zemb et al., 2020). Profiling of communities based on composition can be achieved through high-throughput sequencing, which

is commonly used to target the variable regions within the 16S ribosomal RNA (rRNA) gene or Internal Transcribed Spacer (ITS) region for prokaryotes and fungi, respectively (Preheim et al., 2013). While less commonly employed, functional genes may also be targeted. Sequence processing pipelines have become fairly streamlined and software platforms, such as QIIME2 (Bolyen et al., 2018) and DADA2 (Callahan et al., 2016), ultimately allow the translation of sequences to amplicon sequence variants (ASVs), the microbial approximation of a species (Callahan et al., 2016). The utilization of curated databases can also assign taxonomy to varying degrees of certainty (Nilsson et al., 2019; Yoon et al., 2017), affording more meaning to community profiles and allowing exploration of functional potential (Nguyen et al., 2016). However, due to our limited ability to culture and comprehensively study most soil organisms (Overmann et al., 2017), taxonomic assignment is fairly limited. Amplicon sequence data may also be used to calculate phylogenetic relatedness within and across samples.

Numerous studies over the last two decades have utilized these methods to describe microbial composition and diversity metrics in the context of comparing primary versus perturbed environments. Nonetheless, a more comprehensive community analysis can be achieved by sequencing *all* community DNA, rather than targeting genes of specific microbial groups, a strategy called metagenomics. In most cases, metagenomics avoids the issue of potential PCR bias incurred by amplicon-based studies, and also allows simultaneous analysis of taxonomic/phylogenetic diversity and function from a single dataset (Mendes et al., 2017; New and Brito, 2020). Because no specific gene is being targeted by amplification, comparative analyses can be semi-quantitative as well as compositionally descriptive.

3.2 Defining soil microbial diversity

The magnitude of soil microbial diversity has been gradually realized over the past few decades (Gans et al., 2005; Torsvik et al., 1990). Still, complete characterization has remained elusive, despite the ability to obtain hundreds of millions of DNA sequences from a single sample. Comparative studies among various ecosystems unequivocally show that microbial diversity in soil is the greatest of any environment on Earth (Locey and Lennon, 2016). There are an estimated 100–9000 distinct prokaryotic taxa (bacteria and archaea; operationally referred to as ASVs) per cubic centimeter of soil, constituting approximately 4–20 billion cells. Fungi are relatively less diverse

with approximately 200–235 taxa and 10,000 individuals per gram soil on average (Bardgett and van der Putten, 2014).

The diversity of soil microbial communities is comprised of (1) the total number of distinct taxa/ASVs (richness) and (2) how proportionally abundant (evenness) they are in the environment (Shade, 2017). The use of common diversity metrics borrowed from community ecology, such as alpha (within a sample) and beta (across samples of an environment) diversity (Whittaker, 1972), allows statistical testing of differences in community composition from the local to the landscape scale (Maron et al., 2011). These metrics provide a mechanism to account for spatial heterogeneity effects on community structure at different scales, and furthermore allows comparison across ecosystems and changing environmental conditions. Ultimately, characterization of microbial communities using these metrics is done in an attempt to extend theoretical frameworks used for macroscale populations down to the microscale (Shade, 2017).

Another particularly important aspect of microbial community diversity in soils is the relative abundance of identified species within diverse ecosystems (Gaston, 1994). Variation in the prominence of organisms over time or space may indicate a differential ecosystem function or suitability. Assessing relative changes in the abundance of all organisms across space or environment type provides a metric of community dissimilarity. The variation in community dissimilarity with geographical distance is known as the distance-decay relationship (Bell, 2010) and it is particularly informative when comparing and contrasting environments such as primary forests and pastures. Differences in the distance-decay relationship indicate that disturbance affects the turnover of species across space and provides information about differential taxa dispersal abilities. For example, taxa capable of a broad distribution across soil samples, known as generalists, may be governed by life-history strategies that allow increased dispersal, while specialist taxa are restricted to certain environmental conditions and have limited dispersal (Barberan et al., 2012; Sriswasdi et al., 2017).

Finally, any sound definition of soil microbial diversity requires the understanding of its functional diversity, defined as variation in traits between taxa (Escalas et al., 2019). Ecological traits, however, encompass a variety of ecosystem-relevant functions, such as biogeochemical processes (e.g., methanogenesis, denitrification, biological nitrogen fixation, C utilization, etc.) or cellular regulation processes like stress response. Each of these pathways and processes requires traits that vary in complexity and require intricate genetic machinery in order to be carried out (Martiny

et al., 2015). Therefore, assessment of functional profiles, either through gene-targeted sequencing or metagenomics is essential for gaining a deeper understanding of biogeochemical shifts, as well as for gauging the potential for community resilience or multifunctionality under land-use change.

4. How has land-use change impacted microbial communities in the Amazon?

The following sections will discuss what is known to-date concerning the impacts of land-use alteration on the diversity, community composition, and functional potential of soil microbiomes in the Amazon Rainforest. Studies discussed have focused on several aspects of the microbial community using a variety of analysis techniques across a limited number of established locations (Table 1 and Fig. 2). This creates continuity of datasets and ease of repeated sampling, but imparts regional bias when assessing impacts of soil properties, climate, and land management, an important consideration when comparing results.

4.1 Shifts in community diversity

The first culture-independent study of soil microbial biodiversity in unaltered Amazon Rainforest was reported by Borneman and Triplett (1997) with sequencing of 98 bacterial 16S rRNA gene sequences from two different forest soils in the Brazilian State of Pará. The authors observed that all sequences were unique, and further estimates of species richness concluded that proper assessment of diversity would require sampling over 10,000 sequences per sample (Schloss and Handelsman, 2005). Contradicting the above results, subsequent investigation suggested that Peruvian Amazon soils contain the lowest diversity among soil samples collected across North and South America (Fierer and Jackson, 2006; Lauber et al., 2009). These previous studies, although important, were limited to a few samples.

Early analysis of the effects of deforestation on microorganisms showed that total microbial biomass increases with pasture conversion, and that microbial community structure under land-use change is significantly different from communities of primary forest (Cenciani et al., 2009). These differences were more pronounced in the dry season compared to the wet season. A study using a T-RFLP fingerprinting approach indicated that within-sample (i.e., local) biodiversity increased in converted land-use systems, both in pasture and agricultural plots (da C Jesus et al., 2009).

Table 1 Summary of microbial studies discussed in this chapter, investigating the impact of land use conversion from primary forest to pasture in the Amazon on microbial community diversity, composition, function, and activity.

LUS Effect Measured	Parameters Measured	Land Types	Yr since conversion	Köppens Class, Annual Temp, Precip	Soil Type	Location (s)	Finding (*= statistically signif)	Citation
Soil -Phys/Chem prop controls over bact div/comm str	-T-RLFP cloning/seq of bact comm. -Phys/Chem prop	-Active past -Crop -Agrofor	past: 23-25yr	Af 25.7° C 2562mm	Incept	Benjamin Constant, Amazonas State, BR	*Comms shaped by soil attributes, including base saturation, Al^{3+}, pH *past and crop comms more div than Agrofor	(1) Da C Jesus et al. 2009
MB and bact div	-PCR-DGGE of bact comms -MB C -Phys/Chem prop	-Active past -Fallow "capoeira" past	Active: 20yr Fallow: 15yr	Af 25.7° C 2562mm	Kand	Ariquemes, Rondônia, BR (ARMO)	*MB C and N higher in past than pfor and fallow across seasons *Comm diff across LUSs more pronounced in dry vs wet season *DNA profiles related to Al content, and MB C:Total C ratio	(2) Cenciani et al. 2009
Whole comm tax and phylo div, spatial comm turnover	-Pyroseq of 16S rRNA -Phys/Chem prop	-Active past	22yr	Af 25.7° C 2562mm	Kand	Ariquemes, Rondônia, BR (ARMO)	*pfor and past comms are distinct by comp str *Within-sample tax and phylo div inc in past, but more homogenous across space *Acidobacteria dec and Firmicutes inc. in past	(3) Rodrigues et al. 2013
Comp and relative abund of the phylum Verruco-microbia	-Verruco-microbia -specific 16S gene comp -Phys/Chem prop	-Active past	17yr	Aw 25.5° C 2200mm	Kand (r/y pod- lat)	Ariquemes, Rondônia, BR (ARMO)	*Verrucomicrobia div higher in past, esp. subgroup 3 (tax, phylo) *Comp shifts, esp an inc. in subgroup 3 and dec. in Spartobacteria *absolute abund. assoc w/C content	(4) Ranjan et al. 2015
Comp and relative abund of the Acidobacteria phylum	-16S rRNA comm comp -Phys/Chem prop	-Active past	22yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*Acidobacteria are nearly 2x as abund. in pfor as past *Comm. comp. of most abund. subgroups homogenized across past soils	(5) Navarrete et al. 2015

Abund and comm str of Thaumarchaeal ammonia oxidizers	-qPCR of *amoA* gene -Pyroseq Rhaumarchaeal *amoA*, 16S	-Active past	13yr 102yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*Thaumarchaea over 10x lower in past compared to pfor. (per ng DNA), but not correlated w/ Phys/Chem prop **amoA*-based comms less div. **Nitrosotalea* (cluster 4) disappear in past	(6) Hamaoui et al. 2016
Div and comm str of archaeal domain	-PCR DGGE of 16S rRNA gene -clone library of *amoA* gene -Phys/Chem prop	-Crop -Active past	Crops; 2yr; past: 38yr; sugarcane previously	Af 25.7°C 2562mm	Incept	Benjamin Constant, Solimões River, Amazonas state, BR	*Distinct archaeal comms across LUS *Div. of ammonia oxidizing archaea lower in converted LUS compared to pfor.	(7) Navarrete et al. 2011
Comm resp to LUS change and repeated burning	-16S rRNA seq -Phys/Chem prop	-Aband past -Active past -'Area in preparation' -Subsist-ence ag	NP	Af 20-32°C 1700-2000	Typic Hapludalf Hapludult	Tepequém settlement, Amajari, Roraima, BR	-Species rich dec following pfor. burn (conversion to past) -Conventional plantations and intensively managed agriculture have lowest species rich and div.	(8) Melo et al. 2021
Comp and func div as related to soil phys/chem prop	-16S rRNA pyroseq, qpCR -MG -Phys/Chem prop	-Defor sites (slash and burn)	2-4mo.	Am 28° C 2000mm	Ox	Porto dos Gaúchos & Ipiranga do Norte, Mato Grosso, BR	*Dec in SOM, inc in pH, base saturation *Inc in alpha div, Actinomycetales (related to N) *Dec in Planctomycetes (related to Al), Verrucomicobia, Chlamydiae *Inc in DNA repair/ protein maintenance genes	(9) Navarrete et al. 2015a
Rhiz microbe tax and func comp along a LUS chrono-sequence	-MG -Greenhouse experiment to simulate rhiz -Phys/Chem prop	-Crop (no-till)	1, 10, 20yr	Am 27° C 1400mm	NP	Alto Xingú, Querência municipality, Mato Grosso, BR (12°22'S; 52°15'W)	*Homogenization in cropping systems- bulk soil and rhiz *func shifts occur in bulk soil related to virulence, K metab, disease defense *soybean rhiz is stable over time *Al and cation negatively impact tax div metrics	(10) Goss-Souza et al. 2019

Continued

Table 1 Summary of microbial studies discussed in this chapter, investigating the impact of land use conversion from primary forest to pasture in the Amazon on microbial community diversity, composition, function, and activity.—cont'd

LUS Effect Measured	Parameters Measured	Land Types	Yr since conversion	Köppens Class, Annual Temp, Precip	Soil Type	Location (s)	Finding (*= statistically signif)	Citation
Whole comm div and func resp to soil conditions under LUS change	-MG -Phys/Chem prop	-Active past	20yr.	Am 26° C 2150mm	Ox	Tapajós National Forest, Pará, BR (2°51'23.9' S, 54°57'28.4'W)	*Comms have distinct tax between LUS, assoc. w/ soil water holding capacity, but no diff. in rich *past soil comms are more func. div and assoc. w/Al concentration	(11) Pedrinho et al. 2019
Linking func and tax div	-MG -Phys/Chem prop	-Defor -Crop (soy) -past	NP	Am 28° C 2000mm	Ox	Ipiranga do Norte, Mato Grosso, BR	*Alpha div incs, beta div decs in past *Seasonal trends in div more dramatic in defor sites *Tax and func struct diff between defor and pfor sites *Proteobacteria dec, Chloroflexi, Firmicutes inc in defor sites *Virulence and disease resp, aromatic metab genes higher in for, protein metab higher in defor.	(12) Mendes et al. 2015(b)
Catabolic respiration	-Substrate-induced respiration profiles	-Degraded past -Improved past -Crop (no-till) -Crop (till)	Various	Various	Various	Rondônia, Mato Grosso	*Divergent profiles of catabolic resp *pasts respond to carboxylic and amino acids, pfors/cerrado respond to malonic, malic and succinic acid *soil type and climate are less important than LUS	(13) Mazzetto et al. 2016

Func gene comp shifts with LUS change	-GeoChip4.0 gene probe -Phys/Chem prop	-Active past	6yr 38yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*Func. gene rich, and number of gene families dec. in young past (32% lower), but begins to recover in older past (16% lower). Func. gene redundancy higher in past *Denitrification, methane monooxygenase linked to pfor sites *pfor. soil comms have more genes assoc with C fixation and degradation, CH_4 oxidation, N cycling (ammonification, annamox, assimilatory N reduction, nitrification, etc.) *Only pullalanase and isopullulanase were assoc with past sites	(14) Paula et al. 2014
Div of whole fungal comm	-DGGE of 18S rRNA gene	-Active past -Agrofor -Crop	NP	Af 25.7° C 2562mm	Incept	Benjamin Constant, Alto Solimões, Amazon State, BR	*Shift in dominant fungal groups between past and other LUS: Basidiomycota in past, Zygomycota in pfor and crop	(15) Fracetto et al. 2013
AM fungi abund	-Spore count (trap cultures)	-Active past -Agrofor -Crop	NP	Af 25.7° C 2562mm	Incept	Benjamin Constant, Alto Solimões, Amazon State, BR	*trap culture spore counts higher in past than pfor	(16) Leal et al. 2009
AM fungi div	-Spore count -Spore tax -Plant species	-Active past -Agrofor -Crop	41yr (sugarcane prior)	Af 25.7° C 2562mm	Incept	Benjamin Constant, Alto Solimões, Amazon State, BR	*Inc in spore count in past *Inc in spore div/count in crop/agrofor	(17) Sturmer and Siqueira 2011

Continued

Table 1 Summary of microbial studies discussed in this chapter, investigating the impact of land use conversion from primary forest to pasture in the Amazon on microbial community diversity, composition, function, and activity.—cont'd

LUS Effect Measured	Parameters Measured	Land Types	Yr since conversion	Köppens Class, Annual Temp, Precip	Soil Type	Location (s)	Finding (*= statistically signif)	Citation
AM fungi div	-Spore count -Spore tax -Phys/Chem prop -SOM	-Active past	41yr (sugarcane prior)	Af 25.7° C 2562mm	Incept	Benjanin Constant, Alto Solimões, Amazon State, BR	*Inc spore count in past *Comm comp diff	(18) Leal et al. 2013
Fungal/ plant comm relationship	-Fungal rDNA comp -Plant *trnL* comp	-Active past	38yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia (ARMO; 10° 10′5″S and 62° 49′ 27″ W)	*Comp diff with LUS *Basidiomycota dec in past	(19) Mueller et al. 2014
Fungal comm/ distribution patterns across LUS types	-Fungal rDNA comp, richness	-Active past	6yr 38yr 99yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia (ARMO; 10° 10′5″S and 62° 49′ 27″ W)	-Rich decreases in past *Comm comp shifts *Generalist fungi in pasts, regardless of age *Geographical dist from pfor is strong predictor	(20) Mueller et al. 2016
Fungal/plant comm div interaction	-Fungal rDNA comp in litter and soil	-Plantations	Plantation seedlings ~3yr	Af 25.7° C 3041mm	Acrisol	Paracou, French Guinana (5° 18′ N, 52° 53′ W)	-No variation in richs or evenness across plantations or pfor. *High spatial heterogeneity	(21) Schimann et al. 2017
Fungal comm/ phytopathogen prevalence	-Fungal rDNA comp, div	-Active past	NP	Aw 20° C 1600-1900mm	NP	Mutum-Paraná River, Rondônia, BR	*Comp diff with LUS *Div incs in past *Comms more homogenous across past *potential phytopathogens inc in past	(22) Cerqueira et al. 2018

Assembly processes in rhiz comms following conversion	-MG -Greenhouse rhiz -Phys/Chem prop -Enzyme activity	-Crop (no-till)	1, 10, 20yr	Am 27° C 1400mm	NP	Alto Xingú, Querência municipality, Mato Grosso, BR (12°22'S; 52°15'W)	*Comm. assembly in soybean bulk soil fit neutral assembly model *Comm assembly in rhiz fit niche-based model, leading to a point of permanent distribution state	(23) Goss-Souza et al. 2020
Variation in microbial genomes	-Metagenome-assembled genomes (MAGs)	-Active past	38yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*Carbohydrate metab, cell signaling, dormancy genes inc in pasts. RNA metab and cofactor inc in pfor *Methanogensis genes inc, methanotrophy genes dec *Thaumarchaeota disappear in past, tax profiles vary *past comms more tax homogenous *28 MAGs recovered. Several lineages only found in past *Some MAGs from lineages containing no cultured organisms	(24) Kroeger et al. 2018
Bact comm str in relation to soil and litter chemistry	-Bact T-RFLP -qPCR *nosZ, mcrA, pmoA,* 16S -Phys/chem prop	-Active past -Crop (soy)	20+yr	Aw 2000 mm	Red Ox	-Sinop, Mato Grosso, BR	*Inc'd pH, nutrient status, OM lability *Comm str shifts in LUSs -Bact richness does not decrease	(25) Lammel et al. 2015a

Continued

Table 1 Summary of microbial studies discussed in this chapter, investigating the impact of land use conversion from primary forest to pasture in the Amazon on microbial community diversity, composition, function, and activity.—cont'd

LUS Effect Measured	Parameters Measured	Land Types	Yr since conversion	Köppens Class, Annual Temp, Precip	Soil Type	Location (s)	Finding (*= statistically signif)	Citation
Relation of soil Phys/Chem props and bact comm metrics	-Phys/Chem prop -qPCR and T-RFLP of 16S rRNA gene -MG	-Ag field -Defor -Active past	5yr <1yr >10yr	Am 28°C 2000mm	Ox	Ipiranga do Norte, Mato Grosso, BR	*Acidobacteria and Chlamydiae more abund in pfor soil *Firmicutes more abund in past *Nitrospira, Deinococcus-Thermus in crop systems *Actinobacteria in defor sites *Soil chem properties shape bact comms across LUS: pH, C, N, NO_3^-, and K *Al, base saturation index, Mg, Ca are correlated with many phyla	(26) Mendes et al. 2015(a)
Co-occurrence patterns of prokaryotic comms	-16S rRNA seq	-Active past	38yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*co-occurrence networks between pfor and past are distinct. *Modules of larger networks reflect potential shifts in N cycling in past *Props including temp, C/N, and H^++Al^{3+} impact comm comp and network str	(27) Khan et al. 2019
C cycling activity and SOC characterization along a LUS chrono-sequence	- ß- glucosidase enzyme activity - Fourier-transform spectroscopy -POXC	-Active past	100, 39, 24, 7yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*ß- glucosidase activity incs in past soils in absolute terms, but decs when normalized by C content *SOC incs with past age, POXC fraction decs with past age	(28) Durrer et al. 2021
Microbial activity resp, C and N cycling	-MB, MR -Phys/Chem prop	-Plantation, -silvo-past -Active past	NR	Af 24-25° C 2500-4000mm	NR	SW of Caquetá Department, Columbia	*MB C inc in silvopastoral and past systems compared to pfor and plantation *SOC content is a controlling factor of microbial activity	(29) Cruz et al. 2019

Methano-genic and -trophic comm div and life strategy	-MG	-Active past	38yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*Methanotroph taxa and *pmoA* genes lower in past vs. pfor., particularly alpha-Proteobacteria **mcrA* higher in past *ruderal life history (disturbance-specialist) favored in pasts.	(30) Meyer et al. 2017
Relationship between CH_4 production and methanogen/troph comms	-CH_4 flux -amplicon seq, *pmoA* and *mcrA*	-Active past	NP	-2200mm (Rond.) -2000mm (Tapa.)	-Kand (r/y pod-lat; Rond.) -Ults, Oxs, Incepts (Tapa.)	-Ariquemes, Rondônia -Tapajos National Forest, Pará	* CH_4 flux higher in past, particularly Rondônia *Methanotrophic rich/relative abund lower, methanogen richness/ relative abund higher in past *Methangen rich and rel. abund correlate to flux rate *526 past taxa highly assoc w/flux rate compared to 41 in pfor.	(31) Meyer et al. 2020
Active methanotrophic comms	-SIP amplicon seq and MG (methanogens/ trophs)	-Active past	NP	NP	NP	-Ariquemes, Rondônia -Tapajos National Forest, Pará	*Actively-fixing methanogens (particularly acetoclastic types) inc in abund and div in past *Many active taxa id'd in past compared to for	(32) Kroeger et al. 2021
Func potential for C& N cycling	-qPCR of func marker genes: *amoA*, *nirK*, *nirS*, *norB*, *nosZ*, *nifH*, *mcrA*, *pmoA*, 16S, 18SrRNA -Fluxes of NO_3-, N_2O, CO_2, CH_4	-Crop (soy) -Active past	-Crop: 2yr, 25yr -past: 25yr	Am 24.1° C 2171mm	Red Ox with clay texture	-Sinop, Mato Grosso, BR	*Compared to pfor., *nifH, amoA* (bacteria), *mcrA, pmoA, nirK, nosZ* genes dec in past, crop (2yr and 25yr) **amoA* (archaea), *nirS* inc in past, crop (2yr and 25yr) *past is CH_4 source, pfor. and crop are sink or neutral *pfor. is N_2O source, past and crop are neutral	(33) Lammel et al. 2015b

Continued

Table 1 Summary of microbial studies discussed in this chapter, investigating the impact of land use conversion from primary forest to pasture in the Amazon on microbial community diversity, composition, function, and activity.—cont'd

LUS Effect Measured	Parameters Measured	Land Types	Yr since conversion	Köppens Class, Annual Temp, Precip	Soil Type	Location (s)	Finding (*= statistically signif)	Citation
Microbial-mediated C and N cycling across past	-MB C -Soil C,N mineralization/ nitrification -CH_4, N_2O, CO_2 flux	-Degraded past (no pfor. comparison)	-19yr	Am 25. 6°C 2200mm	Ox, Ult	-Fazenda Nova Vida, Rondônia, BR	*MB C varied 8x across pasts. based on soil type *past are either source or sink of CH_4, typically a source of N_2O, and CO_2 efflux loosely related to MB C *High rates of N immobilization for MB growth	(34) Cerri et al. 2006
Changes in soil MB and activity	-MB C -respiration	-Fallow past -Active past	-Fallow: 9yr -past: 2, 6, 11yr	Awi 26°C 2082mm	Dystrophic Ox	Itupiranga, Pará, BR	*Young past contain less C and MB C than pfor and fallow past *Metab quotient highest in young surface pasts. but decreases in older pasts.	(35) Melo et al. 2012
Impact on N cycling on bact comms	-16S rRNA amplicon seq - qPCR (*nifH*, *amo*A, *amo*B, *nir*K, *nos*Z, 16S) -Phys/Chem prop	-Crop (no-till; corn, soy)	2yr 8yr 20yr	Am 26°C 2150mm	Typic Haplustox (Ox)	Tapajós National Forest and Belterra municipality, Pará, BR	*Inc. bact div, dec archaeal div w/conversion *Inc N fixation in young ag soils *Greater potential for N_2O reductase (N_2O ➔ N_2) in crop soils over pfor *Greater potential for nitrite reductase (NO_2^- ➔ NO) in pfors over crop soils *Ca, Al, NH_4^+ and total N correlated to comm str	(36) Merloti et al. 2019

N-cycling comm str, comp and func.	-MG -qPCR of N-cycling genes (*nifH*, *nirK*, *nosZ*) -Phys/Chem prop	-Active past	21yr	Am 26° C 2150mm	Ox	Belterra municipality, State of Pará, BR	*Al saturation and NO_3^- corr w/ tax and func comm str related to N cycling *pasts more func and taxon rich in N cyclers *Enriched taxa include *Anaeromyxobacter, Bacillus, Geobacter, Sorangium, Koribacter, Streptosporangium, and Conexibacter. Mycobacterium decrease* **nifH*, *nirK*, *nosZ* gene counts inc *denitrification gene trends differ by season *ammonia assimilation and nitrosative stress higher in past *nitric oxide synthse lower in past *past soils contain more specialists (unique)	(37) Pedrinho et al. 2020
Isolation of free-living diazs to determine div	-Isolation of culturable free-living diaz + protein profiling -nitrogenase activity	-Agrofor -Crop -Active past	NP	Af 25.7° C 2562mm	NP	Benjamin Constant, Alto Solimões, Amazon State, BR	*Cell densities were highest in past-soil derived cultures for two of three medias tested *Id'd isolates from past included *Burkholderia* and *Bacillus* *nitrogenase activity varied, but highest performer id'd from past soil only	(38) Silva et al. 2011
Viability, div, and efficiency of symbiotic (nodulating) diaz	-Nodulation density and efficiency of promiscuous legume	-Agrofor -Crop -Active past	38yr	Af 25.7° C 2562mm	Incept	Benjamin Constant, Alto Solimões, Amazon State, BR	*Highest nodulation number from agrofor and crop systems, followed by past, and pfor with lowest number *LUS contain similar number of 'efficient' nodule-forming strains, but crop and past contain highest number of 'inefficient; strains. pfor. contained the most 'high efficiency' strains	(39) Lima et al. 2009

Continued

Table 1 Summary of microbial studies discussed in this chapter, investigating the impact of land use conversion from primary forest to pasture in the Amazon on microbial community diversity, composition, function, and activity.—cont'd

LUS Effect Measured	Parameters Measured	Land Types	Yr since conversion	Köppens Class, Annual Temp, Precip	Soil Type	Location (s)	Finding (*= statistically signif)	Citation
Diaz comm div	-*nifH* clone seq -qPCR of *nifH* gene	-Active past	5yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	-Rich and div were not diff *past comm str diff taxally and phylo *More gene copies in past than pfor *Diaz Firmicutes enriched in pfor, Spirochaetes, delta-proteobacteria, Verrucomicrobia and uncultured favored in past	(40) Mirza et al. 2014
Distance-decay relationship of diaz comms	-*nifH* gene seq -Phys/Chem prop	-Active past	38yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia, BR (ARMO)	*Local (alpha) div incs, but comm turnover (beta) decs *LUS was a stronger determinant of comm str than geographic dist or Phys/chem prop *Pfor is particularly dissimilar w/ dist phylo	(41) Mirza et al. 2020
Impact of fire frequency	-N_2 fixation rates -Soil Phys/Chem prop	-Pfor stands of variable fire frequency	NA	Aw 26° C 2000mm	NP	Araguaia State Park, Mato Grosso, BR	*Fire history decs N fixation rate in pfor areas, on average 24% -Frequency of fire has no signif effect *Positive linear relationship between N fixation rate and C:N ratio and P content in unburned For - Relationship between these factors was nonlinear in burned For.	(42) Bomfim et al. 2020

Abbreviations: Aband: Abandoned.**Abund:** abundance/ abundant. **Agrofor:** Agroforestry. **Al:** aluminum. **AM:** Arbuscular mycorrhizal. ***amoA*:** ammonia monooxygenase gene. **ARMO:** Amazon Rainforest Microbial Observatory. **Assoc:** associated. **Bact:** bacteria. **BR:** Brazil. **C:** carbon. **CH_4:** methane. **Comm:** community. **Comp:** composition. **Crop:** Agricultural cropping system. **Dec:** decrease. **Defor:** Deforested. **Diaz:** diazotrophic. **Diff:** difference. **Dist:** distance. **Div:** diversity/diverse. **Esp:** especially. **Func:** functional/function. **Inc:** increase. **Incept:** Inceptisol. **K:** potassium. **Kand:** Kandiudult. **LUS:** LUS systems. ***mcrA*:** methyl coenzyme M reductase gene. **MB:** microbial biomass. **Metab:** metabolism/metabolic.**MG:** Metagonomic profile (DNA-based). **MR:** microbial respiration. **N:** nitrogen. **NA:** Not applicable. ***nifH*:** nitrogenase reductase. ***nirK*:** nitrite reductase gene. ***nosZ*:** nitrous oxide reductase gene. **NP:** Not provided.**Oxisol:** Oxisol. **Past:** pasture. **PCR DGGE:** polymerase chain reaction denaturation gradient gel electrophoresis. **Pfor:** primary forest. **Phys/Chem prop:** Physicochemical properties. ***pmoA*:** particulate methane monooxygenase. **POXC:** permanganate oxidizable carbon. **Phylo:** phylogenomic/phylogenetic. **Precip:** precipitation. **Pyroseq:** pyrosequencing. **qPCR:** quantitative Polymerase Chain Reaction. **Resp:** response.**Rhiz:** rhizosphere. **Rich:** richness. **r/y pod-lat:** red-yellow podzolic latosol. **Sfor:** secondary forest. **Seq:** sequencing. **Signif:** significant. **SOC:** soil organic carbon. **SIP:** Stable Isotope Probe. **SOM:** soil organic matter. **Str:** structure/structural. **Tax:** tax/tax. **Temp:** Temperature. **T-RLFP:** terminal restriction length fragment polymorphism. ***trnL*:** chloroplast intron gene. **Ult:** ultisol.**Yr:** year/s. **16SrRNA:** prokaryotic ribosomal RNA gene (DNA-based)

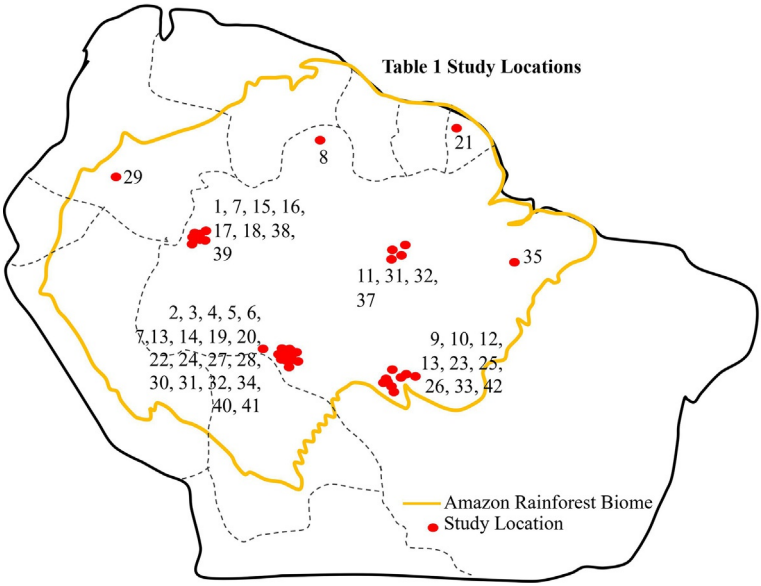

Fig. 2 Geographical distribution of studies presented in Table 1. Labels correspond to number in "Citation" column.

Local-scale response to land-use change is therefore seemingly divergent between macro- and microbiota, and this result could be interpreted as implying that microbial diversity should be excluded when assessing biodiversity losses in tropical systems. However, this is only part of the story.

In 2009, our group created the Amazon Rainforest Microbial Observatory (ARMO) to expand upon the understanding of soil microbial response to forest-to-pasture conversion. Using a nested quadrat, we collected soil samples that spanned centimeter to kilometer intervals from primary forests and actively grazed pastures in the western Amazon, State of Rondônia, Brazil. The area was selected because it represents an extreme case of agricultural development, with higher total deforestation rates than any other state in the BLA. The spatially-explicit sampling scheme allowed for the assessment of not only microbial richness as a measure of alpha diversity, but also community compositional variation and turnover as components of beta diversity. Contrary to the hypothesized trends, our research has shown that local taxonomic and phylogenetic richness increase with forest-to-pasture conversion. Spatially, forest communities turn over (i.e., become more dissimilar) much more rapidly with increasing distance between samples, while pasture communities are fairly homogenous, particularly phylogenetically (Rodrigues et al., 2013). This process of increasing

the similarity of community members over space and/or time in the pasture was not the result of taxa invasion (e.g., microorganisms with increased dispersal abilities), but was mainly due to losses of endemic taxa from forest communities and increases in the range of existing taxa. This pattern of loss also drives overall distinct structural changes in the community. A temporal study in Ipiranga do Norte, Mato Grosso, also measured consistently higher alpha diversity, but found much greater seasonal variation in community diversity of pastures compared to forests, potentially indicating more severe seasonal stressors, such as higher exposure to rain and solar effects in pasture soils (Mendes et al., 2015b). The finding of increased alpha diversity with pasture conversion has been shown elsewhere as well (Mendes et al., 2015a; Navarrete et al., 2015a; Pedrinho et al., 2019) but in some cases overall diversity metrics and taxonomic richness show disparate trends (Pedrinho et al., 2019), indicating that community evenness may decline. Other studies have found that taxonomic richness does not change (Lammel et al., 2015b) or even declines (Melo et al., 2021).

This pattern of biotic spatial homogenization with forest conversion has been mirrored in other studies, including in total bacterial communities of converted pastures across cerrado and rainforest biomes (Lammel et al., 2015b), active pastures of Ipiranga do Norte, Mato Grosso (Mendes et al., 2015b), and converted no-till cropping systems in Querência municipality, Mato Grosso (Goss-Souza et al., 2019), as well as within communities of the phylum Acidobacteria in ARMO pastures (Navarrete et al., 2015b), and whole fungal communities in the Mutum-Paraná River Basin (Cerqueira et al., 2018). This trend has held across a range of pasture ages, soil types, climates, and locales (see Table 1 and Fig. 2), indicating that the conversion of forest to pasture, the common factor in each study, is likely the *driving* factor in spatial diversity shifts. The finding of spatial microbiotic homogenization along with monospecific transformation of the aboveground floral community is perhaps unsurprising. However, the functional implication of this spatially-dependent shift in biodiversity is not clear; taxonomic and phylogenetic diversity as metrics offer, at best, limited indication of shifts in relevant ecosystem functions including greenhouse gas and nutrient cycles.

4.2 Shifts in community composition

The shift in community composition across a land-use or disturbance gradient is a distinct measurement from diversity change, that is, communities may be just as diverse but experience significant shifts in the abundance

of some taxa relative to others. Assessing consistency of trends in taxonomic shifts across studies (especially conducted at different locations) may identify taxa particularly responsive to forest-to-pasture conversion. Fig. 3 shows a taxonomic network of 16S rRNA gene-based community member (bacteria and archaea) relative abundances from soils sampled in three forests and three pastures in Agropecuaria Nova Vida, Rondônia, Brazil (ARMO). Overall, the majority of taxonomic levels show no significant alteration in abundance across land-use types, but more groups are associated with forests compared to pastures, consistent with Rodrigues et al. (2013) findings, which concluded that biotic homogenization in pastures is linked to the loss of endemic species from forests.

In the analysis presented in Fig. 3, the largest taxonomic group significantly associated with pasture soils is the phylum Firmicutes, and specifically the order Bacillales and family Planococcaceae. Conversely, Thaumarchaeota, Acidobacteria, Verrucomicorbia, Gemmatimonadetes, Planctomycetes, and much of the Proteobacteria were found to be significantly associated with forest soils (Fig. 3). An increase in the proportion of Firmicutes, a functionally-broad phylum, has likewise been shown in pastures of the same region sampled several years earlier, implying consistent long-term trends in the shifts of community composition (Rodrigues et al., 2013). A significant favoring of Firmicutes was also detected in pastures of the Tapajos National Forest (Pará, Brazil) relative to primary forests. While this was true year round, differences were particularly pronounced during the wet season (Pedrinho et al., 2019). Similarly, in active pastures of Ipiranga do Norte, Mato Grosso, Firmicutes increased in relative abundance by three to four-fold compared to primary forest (Mendes et al., 2015a; Mendes et al., 2015b). A T-RFLP-based survey of compositional changes in Benjamin-Constant (Amazonas State) reflected an opposite response, with Firmicutes decreasing significantly in pastures (da C Jesus et al., 2009). Multiple 16S-based studies have reached the same conclusion concerning a significantly decreased proportion of Acidobacteria, a phylum of Gram-negative, nonspore-forming bacteria typically favoring acidic environments (Dedysh and Damsté, 2018) within the prokaryotic community following pasture conversion (Khan et al., 2019; Navarrete et al., 2015b; Rodrigues et al., 2013). Subgroups 2 and 13 in particular showed a consistent trend, and reflected patterns of spatial biotic homogenization noted by whole community analysis (Navarrete et al., 2015b; Rodrigues et al., 2013). A survey of the response of Verrucomicrobia to land-use change in the same region using phylum-targeted sequencing generally showed greater diversity and relative abundance of subgroup 3 in pastures, but also

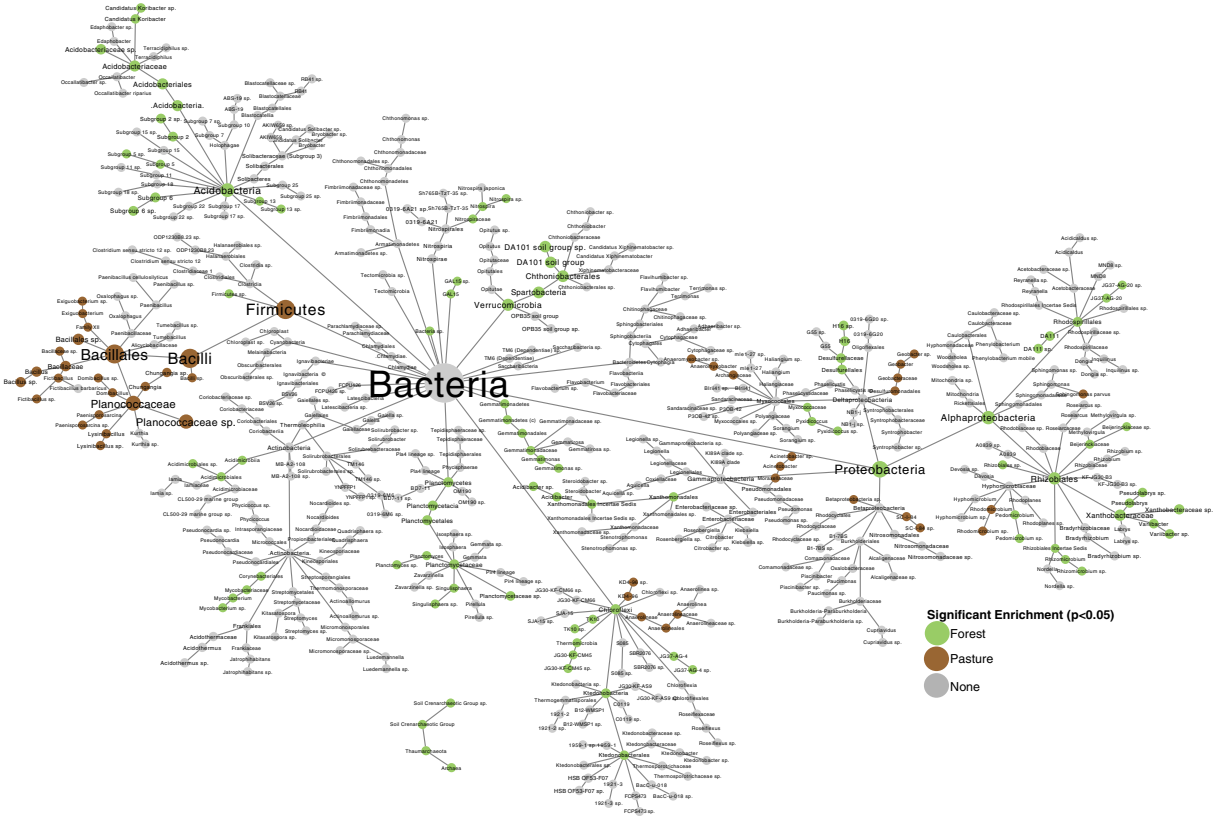

Fig. 3 Hierarchical taxonomic network of prokaryotes (bacteria and archaea) identified in forest and pastures in Rondônia, Brazil based on 16S rRNA sequencing. Three forests and pastures each were sampled at 7 points within a 100 m^2 plot (0–10 cm in depth). Taxonomy included in analysis were subset based on presence in $\geq$50% of total samples, and overall abundance $\geq$0.01% of total sequences. Sequences are pooled to the lowest taxonomic level they are identified to. Text and node size scale with total abundance across samples. Edge length is arbitrary to allow sufficient visual separation of taxonomic groups and is not representative of phylogenetic relatedness. At each taxonomic level, a two-sample Bayesian *t*-test was used to determine a whether abundance differed significantly between forest and pasture. *P*-value of each test were adjusted using a Benjamini-Hochberg correction for multiple comparisons. Taxonomic levels with *p*-values below 0.05 follow correction have nodes colored green for forest association, brown for pasture association, or gray if no significant association is present.

found a significant favorability of the class Spartobacteria in forests, consistent with Fig. 3 (Ranjan et al., 2015; Rodrigues et al., 2013). While the comparison of relative abundance in Fig. 3 suggests favorability of Verrucomicrobia in forests, absolute quantification indicates proliferation with pasture conversion (Ranjan et al., 2015). Despite differences in sequencing techniques and pasture age, the agreement of findings from various studies conducted in the same geographic area builds confidence in its biological reality.

Using deeply sequenced metagenomic profiles, Kroeger et al. (2018) found significant abundance changes in 13 of 34 dominant phyla across forests and ca. 38 year old pastures of the ARMO site. Gemmatimonadetes, Fusobacteria, Aquificae, Lentisphaerae, and Korarchaeota were among phyla identified as being significantly negatively impacted by forest-to-pasture conversion. Additionally, the abundance of Thaumarchaeota, an archaeal phylum containing many known ammonia-oxidizers, was extremely low in pasture communities, in agreement with Fig. 3 as well as Hamaoui et al. (2016) and Khan et al. (2019). Nitrospirae, a small bacterial phylum containing some lineages of nitrite-oxidizing bacteria, was also significantly negatively impacted by pasture conversion (Khan et al., 2019; Kroeger et al., 2018; Rodrigues et al., 2013). These results are not surprising since several members of the plant genera *Brachiaria* and *Urochloa*, common forage grass species in Amazonian pastures, are known to secrete a nitrification-inhibiting cyclic diterpene called brachialactone from roots. This compound works by blocking ammonia monooxygenase and hydroxylamine oxidoreductase enzymatic pathways, limiting NO_2^-/NO_3^- formation and energy production for these chemolithotrophs (Subbarao et al., 2009).

Across the studies discussed, differences in the responses of taxonomic abundance (sometimes reflecting opposite trends) with respect to land-use differences may be due to variability in locale, management, age since conversion, or operational variation such as different sequencing conditions, sample replication, and sequence processing. However inconsistent responses among studies may also be random, pointing to a poor understanding of microbial ecology. Further, explaining the compositional shifts observed is difficult. Thaumarchaeota and Nitrospirae are relatively narrow taxonomic groups with high intra-phylum functional similarity. Drawing inference regarding mechanistic controls over shifts in the relative abundance of Thaumarchaeota and Nitrospirae in response to land-use change is therefore somewhat straightforward. On the other hand, for much larger prokaryotic phyla, such as Proteobacteria, Acidobacteria, or Firmicutes, intra-phylum functional and physiological diversity is sufficiently high that

few generalizations can be made, obscuring any deeper understanding as to why taxonomic groups may respond to land-use change in a particular way. Since most compositional analyses across land-use gradients in the Amazon have been done via 16S rRNA gene-based amplicon sequencing, inference is limited to relative abundance shifts, further conflating which taxonomic changes are true environmental responses.

4.3 Fungal communities

Studies discussed thus far have focused primarily on assessing the response of prokaryotic (16S rRNA gene-based) or whole microbiotic (metagenome-based) communities to land-use change in the Amazon Rainforest. Although fungi are technically included as part of a whole community assessment, their proportional sequence abundance is typically dwarfed by bacterial-derived sequences. One meta-analysis indicated that bacterial rRNA sequences outweigh those of fungi by 20:1 on average and enzyme-encoding sequences derived from bacteria outweigh those of fungi by 163:1 on average, masking impacts related to important ecosystem functions that fungal communities perform (Bahram et al., 2021). Comparatively few studies have focused specifically on the response of fungal functional guilds or whole fungal communities to land-use change in the Amazon. Nonetheless, fungi are important components of forest and pasture ecosystems alike, with mycorrhizal fungi in particular serving as a symbiotic partner to over 90% of terrestrial plant species (Smith and Read, 2010).

Tropical ecosystems are typically dominated by arbuscular mycorrhizal fungi (AMF) (Schimann et al., 2017). Species richness and diversity of AMF do not appear to be significantly reduced by pasture conversion (Leal et al., 2009; Leal et al., 2013). This result is divergent from ecological theory, as well as a survey across forests of the western Amazon, which found a positive correlation between richness of forest plant communities and AMF from the order Glomerales (Peay et al., 2013; Wardle et al., 2004). This likely reflects an important distinction between how trees and forage grasses interact with AMF. Tropical host trees have been shown to make relatively small numbers of selective associations with AM species, and these associations change depending on the age of the tree (Husband et al., 2002). Conversely, forage grasses, like *Brachiaria*, associate with a wide range of AM species (Rodrigues and Dias-Filho, 1996; Teasdale et al., 2019). Despite similar decreases in plant species richness in alternate

land-use types, including agroforestry and crop systems (in comparison to forest), AM fungal richness and diversity may actually increase in some cases (Sturmer and Siqueira, 2011).

There is also evidence that spore abundance increases with the conversion of primary forest to pasture (Leal et al., 2009; Leal et al., 2013; Sturmer and Siqueira, 2011), which is consistent with the observation that the forage grass *B. decumbens* induces high rates of sporulation (Carneiro et al., 1995). This likely has important consequences for above and belowground biomass productivity (Cavagnaro et al., 2014), and should be studied further in the future. Despite overall compositional and spore count differences between systems, species of the genera *Glomus* and *Acaulospora* are abundant and cosmopolitan across land-use types (Leal et al., 2013; Sturmer and Siqueira, 2011).

Fungal communities as a whole play numerous roles in the soil: they may be community-regulating pathogens, plant symbionts, or important drivers of decomposition-related nutrient cycling (Maron et al., 2011; Martinez et al., 2009; Moore et al., 2015; Treseder and Lennon, 2015). Analysis of whole fungal community response to land-use conversion from forest to pasture reflects similar patterns observed for AMF: communities between land-use types are significantly distinct (Cerqueira et al., 2018; Mueller et al., 2014; Mueller et al., 2016). Similar conclusions were also drawn in comparing primary forest with converted monospecific-plantation fungal communities (Schimann et al., 2017). Plant community composition (but not richness) has been found in some cases to act as a significant driving factor in determining fungal composition (Mueller et al., 2014; Schimann et al., 2017). Conversion of forest to pasture appears to induce a decrease in the beta-diversity of the fungal community, indicating greater spatial homogenization, similar to the response of the prokaryotic community (Cerqueira et al., 2018; Rodrigues et al., 2013). Pastures also appear to favor colonization by generalist fungi, concomitant with decreased species richness and independent of factors such as pasture age (Mueller et al., 2016). This may be the result of greater niche competition by fungi able to tolerate extreme conditions.

Some disagreement in the assessment of fungal response to forest-to-pasture conversion has arisen across studies. While Mueller et al. (2016) and Fracetto et al. (2013) found a significant decrease in taxa richness with pasture conversion, Cerqueira et al. (2018) observed increased diversity overall. In addition, while Mueller et al. (2014) observed a significant reduction of the phylum Basidiomycota in pastures, Cerqueira et al. (2018) and

Fracetto et al. (2013) found increased representation of this phyla in pastures. Differences across studies may be explained by factors such as regionality or seasonality at the time of sampling. Owing to the different functions that soil fungi can provide to an ecosystem, it is imperative that we continue to expand our understanding of how soil fungal communities respond to land-use conversion in the Amazon Rainforest.

4.4 Genomic features and novel organisms

Inclusion of all genetic material in the profiling of Amazon microbial communities allows evaluation of general shifts in taxonomic and functional composition, but also enables broad assessment of genomic features. Metagenomic analysis of soils from forests and pastures in the ARMO site showed clear genomic alterations caused by land-use change (Fig. 4). DNA reads with low GC content (35–55%) appear significantly depleted in pasture soils. This is a nonspecific genomic feature, and the driving force or functional consequence of this pattern across land-use types is not readily apparent. However, bacterial GC content, particularly among Gram-negative bacteria, appears positively correlated with genome size (Li and Du, 2014). Some studies have further shown environmental selection mechanisms on GC content, and specific physiological features, such as aerobiosis, have also been associated with high levels of GC (Foerstner et al., 2005; Naya et al., 2002). Further analysis is needed to understand the significance, if any, of this large genomic shift.

Amplification of soil DNA and subsequent attempts to taxonomically annotate sequences typically result in high proportions of unidentified taxa (i.e., no culture match from publicly-deposited sequences; Bach et al., 2018). In an amplicon-based survey of Verrucomicrobia, nearly half of sequences were unidentified, with disproportionate representation in forest soils (Ranjan et al., 2015). While amplicon or unassembled metagenomic sequence data can provide detailed profiles of functional and taxonomic diversity within a community, sequence data lack information concerning the full genetic potential of community members as well as the ability to describe the genetic potential of novel organisms. However, deep metagenomic sequencing data may be utilized to assemble complete or near-complete genomes from the pool of community sequence reads, known as Metagenome Assembled Genomes (MAGs). Employing this technique on soil communities of Amazon forests and pastures produced 28 MAGs, many of which were exclusively identified in pasture compared

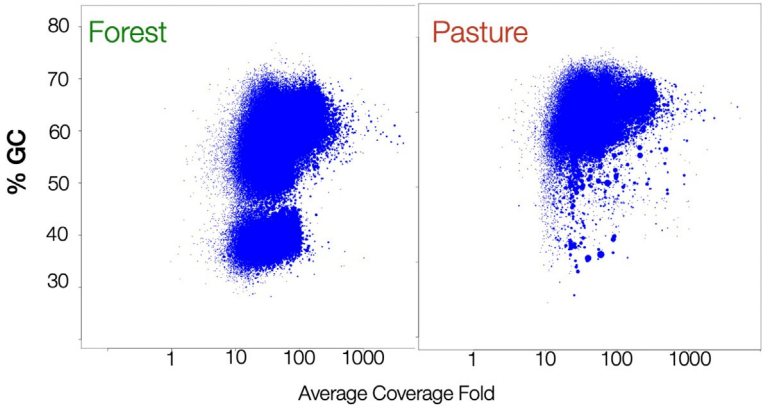

Fig. 4 Coverage of reads at varying GC (guanine and cytosine) content within metagenomes of forest ($n = 5$) and pasture ($n = 5$) of Rondônia, Brazil. Blue dots represent individual reads passing quality filter check. Pasture samples show drastic loss in GC content between 30% and 50%, reflecting strong taxonomic changes. *From J.L.M. Rodrigues, unpublished data.*

to forest samples; just a few were found in exclusively in forest samples (Kroeger et al., 2018). Some MAGs identified within the phylum Acidobacteria were placed in lineages containing no currently cultured organisms, and a phylum Melainabacteria MAG found only in pasture soils was placed within a new lineage in the candidate order Obscuribacter. Additional work exploring MAGs identified very small genomes from the Candidate Phyla Radiation (CPR) Patescibacteria in pasture soils, a vast and previously uncultured group (Nascimento Lemos et al., 2020). The ability of MAGs to recover this unusually small genome calls into question current paradigms concerning the favorability of large genomes in the soil environment, which are based on 16S rRNA gene- or culture-based studies (Nascimento Lemos et al., 2020). Successful recovery of MAGs is computationally limiting, and likely for this reason has not been broadly applied to exploration of land-use change impact on soil microbial communities. However further integration of MAGs into microbial ecology studies could be essential in exploring the unculturable biosphere as well as examining the multifunctional genetic potential of microbial community members.

4.5 Soil physicochemical effects

The physical and chemical conditions of the soil environment have clear impacts on the composition, diversity, and function of microbial

communities. Shifts in these soil-environmental conditions associated with land-use change are in large part what cumulatively shapes microbial community response. Some variables may be affected more strongly by land-use change (e.g., Diochon and Kellman, 2008) or may have a greater impact on microbial communities (Bending et al., 2002; Jones et al., 2019). However due to high spatial heterogeneity even within land-use types (Ritter et al., 2019), physicochemical conditions can also be a confounding factor that should be accounted for. Many soil chemical variables interact with each other: C and N content, for example, have highly constrained ratios in biological tissues (Cleveland and Liptzin, 2007). pH affects the availability of several other soil nutrients such as phosphorus (P; Penn and Camberato, 2019). Additionally, the chemical or structural composition of substrate pools may be an important consideration, even if absolute pool size is unaltered (Ng et al., 2014).

Tropical soils require unique regional considerations in determining the impacts of land-use change on soil physicochemical conditions, and subsequently soil microbial communities. The most common soil types found in the BLA are red-yellow podzols and latosols, equivalent to ultisols and oxisols in the United States-based soil taxonomy system (Moraes et al., 1995). These soils are moderately to highly weathered, predominated by secondary minerals, including kaolinite, as well as iron and aluminum oxides, with soil solution pH typically below 6.0 (Kitagawa and Möller, 1980). Aluminum (Al) saturation tends to be high, and cation exchange capacity (CEC) is low, typically $<10\,\mathrm{cmol_c\,kg^{-1}}$ soil (Bernoux et al., 1998; Dalling et al., 2016). The general paradigm concerning nutrient availability in tropical systems, especially lowland forests of the Amazon Basin, is that most nutrients are immobilized in biomass rather than soil, and that P specifically is limiting to net primary production (Dalling et al., 2016; Vitousek, 1984). N is typically considered more abundant in tropical forests, particularly in comparison to temperate systems (Hedin et al., 2009).

Many studies considering the impact of land-use change on microbial communities in the Amazon measure soil environmental variables as covariates, and some consensus has been reached among studies as to important land-use change-related physicochemical factors shaping microbial community response. Across the studies discussed here, Al content is consistently identified as a significant correlate with microbial community metrics. In most cases, Al content varies significantly with overall community structure. This has been reported from several study regions, including Benjamin Constant, Amazonas (da C Jesus et al., 2009), Ariquemes,

Rondônia (ARMO; Cenciani et al., 2009; Khan et al., 2019), Querência municipality, Mato Grosso (Goss-Souza et al., 2019), the Tapajós National Forest, Pará (Merloti et al., 2019; Pedrinho et al., 2019), and across primary forests, crop systems, and pastures ranging from 20 to 40 years since conversion (see Table 1). In one report, Al content was correlated with both community taxonomic and functional structure (Pedrinho et al., 2020). Several diversity metrics have also been shown to correlate negatively with Al content (Goss-Souza et al., 2019). Additionally, saturation index and total content of Al are among the most universally significant correlation factors with abundance of various taxonomic groups across forests and pastures (Mendes et al., 2015a; >Navarrete et al., 2015a). While the precise importance of Al is unknown in the context of forest-to-pasture conversion, in tropical soils a large proportion of exchange sites are likely occupied by acidic cations (H^+ and Al^{3+}). Therefore Al concentration may be an indicator of CEC or soil fertility rather than a direct control over communities (Carvalho et al., 2009). This explanation is supported by a simultaneous correlation of community metrics with base saturation, total soil acidity, and CEC (Khan et al., 2019; Mendes et al., 2015a). Under this hypothesis, microbial communities may be shaped by plant community response to CEC. Alternatively, soil solution exchangeable Al has been shown to correlate negatively with microbial C use efficiency as pH declines below 5.5, and therefore may directly influence microbial community structure and diversity by selecting for organisms able to tolerate this exogenous stress through detoxification (Auger et al., 2013; Jones et al., 2019). Primary forests in the Amazon Basin typically have a soil pH ranging from ~3.8 to ~5.3 (see references in Table 1; e.g., Lammel et al., 2015b; Mendes et al., 2015a; Neill et al., 1995; Pedrinho et al., 2019). In land-use transition, slash-and-burn clearing methods typically lead to an increase of several-tenths to over 1 pH unit (potentially crossing the aforementioned 5.5 transition point), with gradual acidification over several decades of use. This may explain community differences both across land-use types as well as in various regions of the basin.

In some reports, pH is also an important factor influencing the attributes of microbial communities such as compositional structure and phylum-level taxonomic abundance (da C Jesus et al., 2009; Lammel et al., 2015b; Mendes et al., 2015a). The community composition of AMF across a forest-to-pasture land-use gradient in the same region has also been shown to correlate significantly with pH (Leal et al., 2013). Studies across many other ecotypes have similarly shown pH to be an important determinant of fungal and

bacterial communities, likely because it serves as a control over multiple soil conditions including nutrient availability and mobility, exoenzyme activity, and concentration of cellular stressors (Jones et al., 2019; Lauber et al., 2009; Puissant et al., 2019; Rousk et al., 2010). Mechanistically, moderate ash-induced increases in soil pH following slash-and-burn conversion of forest to pasture may be responsible for the frequently observed increase in local community diversity and richness (e.g., Rodrigues et al., 2013), since this theoretically allows for greater nutrient availability and release from growth constraints (i.e., stressors) imposed by the preexisting acidic conditions in primary Amazon Rainforest soils (de Souza Braz et al., 2013). Concentrations of nutrients and enzymatic co-factors including P, K, S, Ca, Mg, Fe, Mn, B, Cu, Zn, and Mo have pH-dependent availability, with the majority of these increasing as pH increases. Availability of these nutrients has also been shown to play a role in shaping microbial communities at the phylum level (Mendes et al., 2015a) and across functional groups (Pedrinho et al., 2020). Stress response has been identified as a significantly divergent functional characteristic across forest and pasture (Pedrinho et al., 2019), but a more in-depth investigation of stress tolerance genes related to pH-dependent cellular toxins, such as Al, may provide additional insights into the mechanisms driving functional assembly of a community across land-use types.

Several other factors including soil C and N content have also been identified as meaningful correlates across studies at the scale of whole communities, as well as prominent phyla (Cenciani et al., 2009; Cerqueira et al., 2018; Navarrete et al., 2015a; Ranjan et al., 2015). This is perhaps unsurprising given the impact these nutrients have on microbial metabolism and the control they exert over biomass stoichiometry (Cleveland and Liptzin, 2007). Soil water holding capacity has additionally been shown to be significantly related to overall nutrient availability and average water content in the soil environment, therefore likely influencing community composition through differential preferences and tolerances for soil moisture conditions among taxa (Pedrinho et al., 2019; Zhao et al., 2016). The relationship between land-use disturbance, soil physicochemical conditions, and microbial communities is interactive. The response of the microbial community to land-use change is mediated by shifts in the physical and chemical conditions of their environment, which are in turn dependent on pre-existing edaphic and climatic conditions. Therefore, physical and chemical soil attributes are important considerations to understand mechanistic drivers of community change, as well as account for variation in

response on the regional scale. While many studies have measured these variables and analyzed associations with microbial communities across land-use types, our body of knowledge would be greatly improved by hypothesis-driven and experimentally controlled studies in order to draw causal inference.

4.6 Beyond taxonomy: Functional diversity and community interaction

Along with obtaining an inventory of taxa altered by ecosystem disturbance, a central goal of studying the microbial communities of the Amazon Rainforest is to understand their role in mediating soil biological processes. The first comprehensive study of the functional gene diversity of soil microbial communities under land-use change in the Amazon was performed at the ARMO site. The study took advantage of the GeoChip 4.0, a microarray containing 83,992 probes targeting 410 gene families associated with the biogeochemical cycles of C, N, P, and S (Tu et al., 2014). This high-throughput microarray approach detected genes for 409 different families, underscoring the general richness of genes present in Amazon soils. However, reported losses of total gene richness with conversion of primary forest to young pasture (~6 years old) were significant—up to 31.8% (Paula et al., 2014). Genes related to C and N cycles, particularly to the processes of methane oxidation, nitrification, and denitrification, were significantly associated with forest sites while their abundances were reduced in pastures. Such a dramatic, negative shift is compelling since local-scale taxonomic diversity increases with pasture conversion (Rodrigues et al., 2013). In contrast, a metagenomic-based study in the Tapajós National Forest, Pará, Brazil, found that functional diversity increased significantly in conjunction with taxonomic diversity (Pedrinho et al., 2019).

Further, ARMO metagenomes have revealed that carbohydrate metabolism, sporulation, and cell signal regulation functional genes were significantly more common in pasture, while RNA metabolism and cofactors, vitamins, and pigments-related functional genes were more prevalent in forests (Kroeger et al., 2018). These functional profile shifts with land-use change are consistent with another study conducted in the Tapajós National Forest, Pará, Brazil, where the same trends hold true in microbial communities across both the wet and dry season (Pedrinho et al., 2019). The consistency of these studies is intriguing, but future work is needed to connect these broad community functional shifts to taxonomic representation in the context of land-use change, in order elucidate the mechanistic

underpinnings that drive community response. Using metagenomic profiles, Pedrinho et al. (2020) assessed the ecological response of N-cycling community members to land-use change and determined structural alterations associate significantly with (perhaps unsurprisingly) nitrate (NO_3^-) and ammonium (NH_4^+) concentrations. Further, pasture communities contained a high proportion of specialists compared to primary forests.

An aspect of soil microbial ecology that is exceedingly difficult to study through experimentation is functional interactions among taxa. Instead, statistical methods are employed to infer interactions based on co-occurrence across samples, a potential indication of shared niche habitation between taxa. Forests and pastures of Rondônia have distinctly different co-occurrence networks that self-sort by land-use type (Khan et al., 2019). Additionally, nodes clustering taxa by the same functional potential suggests shifts in soil N cycling with land-use conversion (Khan et al., 2019), which is supported by a network analysis performed by Pedrinho et al. (2020). Analysis of rhizosphere versus bulk soil communities in soybean fields converted from primary forest suggest directional, niche-based assembly of communities near roots, compared to neutral (i.e., randomized) community assembly in bulk soil (Goss-Souza et al., 2020), but no such analysis has yet been done to compare forest and converted systems. Functional shifts in soil communities with land-use conversion are clear, but more process-based focus is needed to fully understand nutrient cycle shifts and explain variation across studies.

5. Microbial impacts associated with carbon cycling

The vast expanse of the Amazon rainforest makes it a critical global carbon storage hotspot. However, the initiation of forest-to-pasture conversion through biomass burning definitively leads to a net loss of C per area of former forest. While aboveground biomass accounts for an estimated 400 Mg C stored per hectare of primary forest across the basin (mainly in trees with >10 cm breast-height diameter), pastures store less than one-sixth of this, approximately 63 Mg C per hectare (Hughes et al., 2002; Nascimento and Laurance, 2002). Taking into account soil class-specific differences in organic matter content and distribution across the Amazon Basin, average C density within primary forest soils has been estimated at 98–103 kg C per hectare—on a similar scale as the aforementioned aboveground stocks (Batjes and Dijkshoorn, 1999; Moraes et al., 1995). Fifty-two percent of C stocks are estimated to be held in the top 30 cm

of soil, which are most susceptible to disturbance with land-use conversion (Batjes and Dijkshoorn, 1999). However the net impact of land-use conversion on soil C is far less clear as compared to impacts on plant biomass-stored. Various studies have found that soil C increases (de Moraes et al., 1996; Durrer et al., 2021; Neill et al., 1997a), decreases (Fearnside, 1997; Maia et al., 2010), or does not change appreciably (Durigan et al., 2017; Rittl et al., 2017) following land-use conversion. This suggests that the impact of land-use change on soil C storage is dependent either on pre-existing conditions, such as initial C stocks, soil texture, and nutrient status, or management factors such as the frequency of burns or grazing intensity. In addition, aspects of the microbial community, including net carbon use efficiency, microbial biomass, and genetic potential for degradations are likely relevant.

5.1 Respiration, microbial biomass, and C degradation

Across pasture chronosequences in Rondônia, Brazil, soil C concentration consistently shows an increase with pasture age, and isotopic $\delta^{13}C$ values become significantly less negative, indicating gradual turnover of forest-derived C and replacement with pasture-derived C (Durrer et al., 2021; Neill et al., 1996). Yet, the change in $\delta^{13}C$ value of microbial respiration greatly outpaces that of soil C stocks; in one study, for example, pasture-derived C of 3-year-old pastures constituted 17% of soil stocks, but 69% of microbial-respired C (Neill et al., 1996). This indicates that microbial activity in pastures is driven primarily by fresh inputs, including root exudates and root and shoot tissue. Another study found accumulation of pasture-derived C to be highest in the particulate organic matter fraction (Lisboa et al., 2009), again indicating that elevated proportions of pasture-derived organic C are either respired or converted to biomass before accumulation in smaller fractions. The mechanisms driving retention of forest-dervied C are unclear, but losses appear to be greatest from the silt-sized soil fraction, suggesting soil texture has an interactive role in C storage dynamics under land-use change.

Microbial activity has also been shown to depend heavily on total soil organic C content and pasture age, with metabolic quotients (respiration per unit biomass) highest in young, surface-soil pastures (1–2 years old, 0–2 cm in depth) which contain lower total (and presumably) pasture-derived C as well as lower microbial biomass (MB) C compared to primary forests or older pastures (Melo et al., 2012). Older pastures in this study

(5–12 years) did not accumulate significant soil C or MB C, but metabolic quotients did return to reduced levels similar to forests, indicating shifts in C usage by microbial communities over time as soil pools change in their quality and composition. Other studies have found that MB C typically increases at depths to 20 cm with pasture conversion and variable pasture age (Cenciani et al., 2009; Cruz et al., 2019). Overall, however, concentrations of MB C across pastures may vary eight-fold based on season (dry versus wet) and soil type, accounting for differences across studies and potentially influencing how microbial communities respond to land-use change (Cerri et al., 2006).

Community profiles of catabolic metabolism using substrate-induced respiration across forests and pastures have confirmed differential activity under varying land-use types, with forest communities responding to malonic, malic, and succinic acid, and pasture communities responding to carboxylic and amino acids (Mazzetto et al., 2016). Correspondingly, shifts in the functional profiles related to carbohydrate metabolism derived from metagenomes (Kroeger et al., 2018) further indicate that microbial communities respond to differential organic-matter profiles across land-use types. Among annotated protein-encoding reads of metagenomes, a decrease in lignin-degradation genes, such as superoxide dismutase, was observed in pastures compared to forests (Kroeger et al., 2018). Further, the chemical-structural composition of soil organic matter (i.e., substrate) changes with forest-to-pasture conversion, resulting in an increased concentration of hemicellulose and a decreased concentration of lignin in pastures compared to primary forest, even if total pool size is unchanged (Lammel et al., 2015b). Additionally, pasture soils contain a significantly higher concentration of permanganate-oxidizable C, which serves as an indicate of easily-catabolized C (Durrer et al., 2021). Several other metagenomic-based studies reporting bulk annotation of genes related to degradation of aromatic compounds did not find differences between land-use types (Mendes et al., 2015b; Pedrinho et al., 2019). Paula et al. (2014) found that abundance of C degradation-associated genes was negatively impacted in young (6-year-old) but not older (38-year-old) pasture compared to forests. The young pasture sampled in this study demonstrated significant overall decline in functional diversity, which may be indicative of an important time-dependent response. However, more intermediary-aged pastures between 6 and 38 years old are needed to test this theory. In future studies, shifts in gene expression rather than presence may prove more useful in characterizing soil microbial processes related to C degradation.

Overall, understanding how land-use change impacts C degradation and storage in Amazon soils is limited by a dearth of hypothesis-driven studies and a poor understanding of the relationship between community activity and genetic profiles related to C metabolism. Due to the relatively narrow scope of genes and microorganisms involved in its cycling, the impact of land-use change on methane flux in the Amazon has garnered far more attention and is better understood in terms of ecosystem-scale consequences and functional underpinnings.

5.2 Methane flux

Methane (CH_4) is a climatically-relevant gas with a potency 34 times that of carbon dioxide over 100 years (Myhre et al., 2013). The impact of forest-to-pasture conversion on methane flux has shown consistent trends across the Amazon Basin. Process-rate studies in Rondônia (Western Amazon) and Pará (Eastern Amazon) have shown steady, annual sink-to-source trends with conversion from forest ($-470\,mg\,CH_4\,m^{-2}$) to pasture ($+270\,mg\,CH_4\,m^{-2}$), but no clear trend in emissions has been found with respect to time since pasture conversion (Steudler et al., 1996). Another study across a conversion chronosequence in Paragominas (Eastern Amazon) found that pastures appear to return to a methane sink as they age (Verchot et al., 2000). A previous study has also indicated a consistent sink and source status across all seasons in forests and pastures, respectively, and that pastures act as a much stronger source in wet seasons (up to $+614\,mg\,CH_4\,m^{-2}\,year^{-1}$, or $+1682\,\mu g\,CH_4\,m^{-2}\,day^{-1}$) compared to dry (Fernandes et al., 2002). Measurements conducted in the same region approximately two decades later confirmed pastures to be a persistent source of methane averaging $3454 \pm 9482\,\mu g\,CH_4\,m^{-2}\,day^{-1}$ (Meyer et al., 2020). However, Meyer et al. (2020) found that forests were also a weak source of methane ($9.8 \pm 120.5\,\mu g\,CH_4\,m^{-2}\,day^{-1}$). Another investigation in Sinop, Mato Grosso (Southern Brazilian Amazon) found net daily efflux rates from a 25-year-old pasture of $1104\,\mu g\,CH_4\,m^{-2}$ and low daily uptake rates ($-168\,\mu g\,CH_4\,m^{-2}$) from primary forest (Lammel et al., 2015a).

An early study focusing on process rates and physicochemical shifts in soil profiles under land-use change concluded water-filled pore space to be the key factor in sink-to-source transition of converted pastures, with ~40% filled pores considered the tipping point (Steudler et al., 1996). Indeed, oxygen concentration (inversely related to water-filled pore space)

has been demonstrated to be an important influence over production (Yang and Chang, 1998). The proposed mechanism of an altered methane cycle is that soil bulk density increases with pasture conversion due to cattle movement. This causes a decrease in soil porosity and fractures soil aggregates (Reiners et al., 1994), increasing the frequency of oxygen-devoid microsites that favor the anaerobic process of methane production (Fernandes et al., 2002). However, this physicochemical-focused understanding ignores the direct and indirect impacts of forest conversion on methane-cycling soil microbial community members. To fully understand the differences in net methane flux with land-use change, the impact on the abundance, structure, and activity of soil microbial communities must be considered.

A net flux of soil CH_4 results from a balance between production by methanogenic archaea, and consumption by methanotrophic bacteria (Conrad, 2007). Under anaerobic conditions, CH_4 is generated through the reduction of C1 carbon compounds such as CO2 and methanol or disproportionation of compounds such as acetate (Schäfer, 2013). Methanotrophic bacteria of upland soils, meanwhile, mostly rely on aerobic conditions to oxidize methane to methanol using O_2 as an electron acceptor with either particulate- or soluble methane monooxygenases (Conrad, 2007; Guerrero-Cruz et al., 2021). Although thought to be important mainly in wetland and marine systems, canonical methanotrophic archaea also perform methnotrophy anaerobically, though recent work suggests a greater importance of these organisms to upland soil CH4 cycling than previously thought (Guerrero-Cruz et al., 2021; Ho et al., 2019).

Metagenomic sequencing of forest and pasture soil communities has indicated that CH_4-consuming communities (methanotrophs) are strongly impacted by land-use conversion, with decreased relative abundance and shifted taxonomic composition of methanotroph 16S rRNA genes (Meyer et al., 2017), which confirms a prior GeoChip-based assessment that found a significant association of the abundance of methane monooxygenase genes (denoting methanotrophs) with forests compared to pastures (Paula et al., 2014). In particular, a significant drop in the relative abundance of methanotrophs within the Alphaproteobacteria was detected (Meyer et al., 2017). Furthermore, annotation of community metagenomes of Rondônian soils (ARMO) revealed that all essential genes encoding methyl coenzyme M reductase (*mcr*) were significantly enriched in pasture soils, and particulate methane monooxyenase (*pmo*) genes were significantly

enriched in forest soils (Kroeger et al., 2018). Using a 16S rRNA gene amplicon-based approach confirmed the alteration of functional community patterns across two locations in the Amazon in Rondônia and Pará, with significant increases in methanogen composition and relative abundance, as well as significant decreases in richness and relative abundance of methanotrophs in pastures (Meyer et al., 2020). Similarly, absolute gene quantification has shown a significant increase in *mcrA* ($\sim$2.5 $\times$) and a significant decrease in *pmoA* ($\sim$0.5 $\times$) gene copy numbers per gram soil in pastures compared to forests (Lammel et al., 2015a).

Taking microbial *activity* into account expands on these findings. In the 16S rRNA gene-based analysis discussed above, the flux of CH_4 across soil types appeared to be associated with richness and relative abundance of methanogenic communities after accounting for sample covariate structure (Meyer et al., 2020). Fig. 5, reproduced with permission from Meyer et al. (2020), reflects a positive relationship between both community attributes and CH_4 flux ($R^2 = 0.42$ for both) when land-use types are considered together, but linear relationships appear particularly driven by pasture communities. In another study, an absolute quantitative analysis of CH_4-cycling genes (*mcrA* and *pmoA*) did not show a significant, direct explanatory relationship with flux rates, which did not vary between forest and pasture (Lammel et al., 2015a). This finding may speak to the spatial and temporal heterogeneity of the process. While 526 taxa were highly associated with methane flux in pasture soils, just 41 taxa were associated with flux in primary forest. Moreover, few of these taxa were known methane-cyclers, indicating a wide range of organisms associated or co-correlated with the process, but not directly mediating it (Meyer et al., 2020). Use of an isotopic tracer (^{13}C) to enrich and identify microorganisms involved in CH_4 cycling under a given set of conditions has also indicated an increase in the abundance and diversity of active methanogens in pastures (Kroeger et al., 2021). These results highlight the importance of integrating process-based measurements with microbial community profiles to understand their role in ecosystem function. It should be noted that while the ecology of CH_4 cycling across this large-scale land-use gradient represents a complex and important area of study in soil microbial ecology, the contribution of upland soils only amounts to approximately 5% of the overall CH_4 emissions across the Amazon Basin, with biomass burning and cattle accounting for the major sources (Steudler et al., 1996).

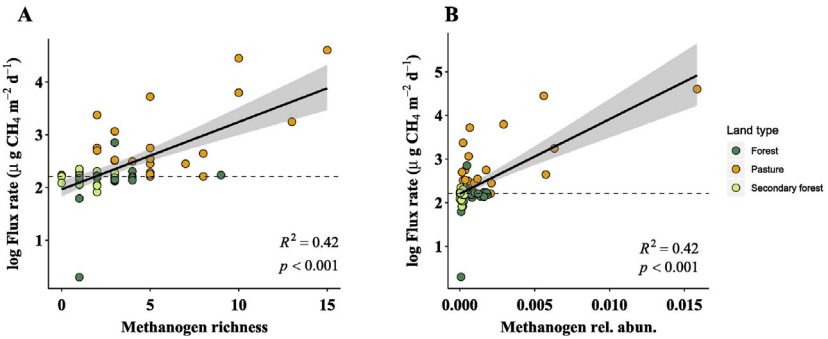

Fig. 5 Figures show significant relationships between (A) methanogen richness and (B) methanogen relative abundance and log-transformed methane flux rate, taken from forest, pasture, and secondary forest in two Amazon states: Rondônia and Pará, Brazil. The R^2 values shown represent the proportion of variance in logarithmic methane flux explained by methanogen richness or relative abundance using a linear model approach. Dotted lines represent a flux rate of 0 μg CH_4 m^{-2} day^{-1} since a minimum value is added to data (+162). *Reproduced with permission from Meyer, K.M., Morris, A.H., Webster, K., Klein, A.M., Kroeger, M.E., Meredith, L.K., Braendholt, A., Nakamura, F., Venturini, A., Fonseca de Souza, L., Shek, K.L., Danielson, R., van Haren, J., Barbosa de Camargo, P., Tsai, S.M., Dini-Andreote, F., de Mauro, J.M.S., Barlow, J., Berenguer, E., Nusslein, K., Saleska, S., Rodrigues, J.L.M., Bohannan, B.J.M., 2020. Belowground changes to community structure alter methane-cycling dynamics in Amazonia. Environ. Int. 145, 106131 and Creative Commons License.*

6. Microbial impacts associated with nitrogen cycling

Nitrogen, an essential nutrient for both plants and soil microorganisms, is tightly linked in its cycling with C through both soil organic matter and biomass. Soil N comprises both organic and inorganic nutrient pools and is utilized for biomass assimilation as well as dissimilatory energetic reactions (Pajares and Bohannan, 2016). A thorough review of N cycling in tropical soils with discussion pertaining to climatic and pedological factors unique to this region is provided in Pajares and Bohannan (2016), although the focus of the review remains on forest ecosystems generally rather than on land-use conversion gradients. Unlike temperate soils which are geologically younger, highly weathered tropical soils are typically considered replete with N, but limited in P and base cations (Hedin et al., 2009). However, disturbance related to pasture conversion may alter this pattern. The reality that a high proportion of pastures are eventually abandoned (Chazdon et al., 2009) presents a pressing need to better understand how microbial communities

mediate N cycling across land-use change gradients. This is especially relevant since N limitation is a suspected contributor to productivity decline. Similar to C pools, total N has been reported to increase (Navarrete et al., 2015b; Neill et al., 1997b), decrease (Lammel et al., 2015a; Neill et al., 1997b; Pedrinho et al., 2020), or remain stable (Durigan et al., 2017; Melo et al., 2012; Neill et al., 1997a) with forest-to-pasture conversion. Regionality, intensity of conversion practices, and pasture age/management could account for many of these differences; however, significant shifts have been reported in both transformation rates and pool sizes of N in pastures (Neill et al., 1996).

Several aspects of land-use conversion to pastures are plausible contributors to the above shifts, which are conceptualized in Fig. 6. Common forage species used throughout pastures in the Amazon are known to exude a nitrification-inhibiting compound called brachialactone as a strategy for scavenging N (Egenolf et al., 2020; Subbarao et al., 2015). It is not clear how soil N availability scales with brachialactone production (e.g., whether exudation is obligate or facultative), but its presence in the rhizosphere is likely to impact community structure and activity of N-cycling soil microbial communities. The effect of cattle grazing in pastures is additionally a relevant consideration. Cattle grazing exports nutrients from the ecosystem through the animal itself, but also through displacement and inefficient nutrient recovery following excretion; this may contribute to N loss through NH_3 volatilization, leaching, or erosion (Dias-Filho et al., 2001). This could cumulatively have a substantial impact on available N supply with a net export being estimated up to $20\,kg\,N\,ha^{-1}\,year^{-1}$ (Dias-Filho et al., 2001). Limited reporting on the relationship between grazing intensity/rotational practices and soil C and N dynamics in tropical systems suggests that soil C and N cycling and storage may be unaffected by light grazing, but depressed under medium or heavy stocking rates (Cantarutti et al., 2002; Silva et al., 2008). Since soil microbial functional groups mediate key steps in the soil N cycle such as nitrogen fixation, mineralization, nitrification, and denitrification, their response to land-use alteration in the Amazon deserves thorough examination to better understand shifts in the N cycle across the region.

6.1 Nitrogen fixation

Nitrogen fixation, the conversion of atmospherically-derived N_2 to a biologically reactive form (NH_3) is an imperative function for providing new N

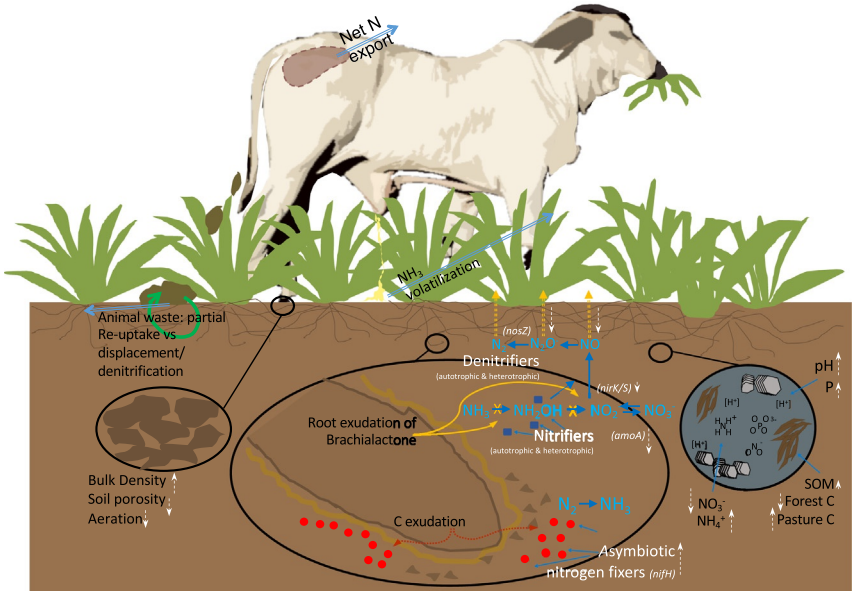

Fig. 6 Crucial shifts occur in the nitrogen (N) cycle with conversion of primary tropical forest to pasture in the Amazon. Evidence from studies compiled so far suggest N is lost from the system upon conversion, and is further lost through cattle grazing, by export of biomass, and potentially inefficient reuptake of animal waste. Additionally, forage grasses such as those within the genera Brachiaria and Urochloa release a nitrification inhibitor called brachialactone from roots which inactivates enzymes catalyzing the oxidation of ammonia (NH_4^+) to nitrate (NO_3^-). This shifts the inorganic N pool from NO_3^--to-NH_4^+- dominated, impacting availability of N for plants and microbes (both for biomass assimilation and redox reactions). Grazing impacts the physical soil environment by increasing bulk density and subsequently decreasing soil aeration and porosity. The shift in plant community has an inconsistent effect on total soil organic matter (SOM) storage across the Amazon. In the decades following conversion, SOM gradually shifts from forest-to-pasture derived, but the fraction actively metabolized by soil microbes is heavily pasture-derived even in very young pastures. pH increases by ash fertilization following forest conversion, potentially releasing microbial and plant communities from nutrient limitations including phosphorus (P). These factors are likely contributors to an observed increase in asymbiotic nitrogen fixers in the rhizosphere, in response to greater N limitation and favorable conditions. Decreased nitrification may also negatively impact nitrous oxide (N_2O) flux via denitrification, though results are mixed on the impacts of land use change on the abundance and diversity of denitrifying microbes.

to terrestrial ecosystems, especially in the early stages of succession. Despite the relative abundance of N in tropical forest soils, both symbiotic and associative/free-living N_2 fixation (SNF and ANF respectively) in soil, leaf litter, and the tree canopy are thought to be important processes in response to

considerable loss through NO_3^- leaching and denitrification, as well as in order to maintain extracellular phosphatase activity required to combat P limitation (Hedin et al., 2009; Pajares and Bohannan, 2016). A key difference in potential diazotrophy with forest-to-pasture conversion is that forage grasses sown in pastures are not leguminous, and therefore do not engage in symbiotic nodulation or SNF. This is likely to have effects on community composition, regardless of N_2 fixation rates. Based on the potential loss of pathways associated with landscape conversion to grazed pastures, it is reasonable to postulate that associative and free-living diazotrophs may have an elevated role in N-cycling (via ANF) following land-use change.

SNF-diazotrophs have the benefit of O_2-depleted conditions (O_2 reversibly inactivates the nitrogenase enzyme) and a direct supply of C and energy from root nodules, in exchange for some of the N_2 they fix. ANF-diazotrophs, on the other hand, are subject to more extreme environmental conditions and must fund the steep energetic cost of ANF themselves. It is then probable that their activity is almost entirely limited to the rhizosphere, where plant root deposits may serve as an easily-utilized C source, stimulating microbial activity (Fig. 6; Bürgmann et al., 2005). The impact of grazing on plant root C allocation appears highly dependent on forage species, grazing intensity, and soil nutrients (Dawson et al., 2000; Hamilton III and Frank, 2001). However, based on limited data, low cattle stocking rates may stimulate belowground C allocation (Dias-Filho et al., 2001; Durigan et al., 2017; Trumbore et al., 1995). Due to high energetic costs, ANF may also be heavily regulated by NH_3 concentration (Peters et al., 2013), bringing into question the potential impact of nitrification inhibition by brachialactone. Depending on the efficiency with which forage species scavenge available NH_3, environmental concentrations may be high enough to inhibit ANF. On the other hand, ANF also requires a supply of N (Peters et al., 2013), so increased NH_3 concentration may stimulate activity in conjunction with C-rich root exudates.

Lima et al. (2009) performed a valuable survey of viability, diversity, and efficiency of symbiotic (nodulating) diazotrophs across primary forests and converted landscapes including pasture. Using a promiscuous legume, nodulation rates were highest in agroforestry soils and lowest in primary forests; however, the most efficient strains (performing SNF in the presence of high N content) were identified from forest soils, whereas pastures were typified by mostly inefficient strains. Given the lack of leguminous plant species in pastures, their continued presence suggests alternative ecological

roles and a strong potential for root colonization in a pasture abandonment/secondary forest succession scenario. A free-living, diazotroph-targeted culture-based experiment found that pasture soils yielded the highest cell densities when compared to primary forest, agricultural, and agroforestry systems (Silva et al., 2011). Subsequent protein profiling identified *Burkholderia* and *Bacillus* among pasture-derived isolates. Nitrogenase activity was variable across strains within and among land-use types, but the highest performing strain was isolated from pasture soils. Due to the inherent limitations of assessing environmental biodiversity using culture-based methods, conclusions from these studies should be taken with care, but serve as a baseline for comparison with molecular-based methods.

Assessment of diazotrophs at the ARMO sites was conducted by sequencing gene clones, as well as directly amplifying the *nifH* gene, which encodes an essential subunit of the nitrogenase enzyme (Mirza et al., 2014; Mirza et al., 2020). Quantitative analysis first indicated a significant increase in *nifH* gene abundance per gram of pasture soil compared to that in forest soil (Mirza et al., 2014), and community structure varied significantly by land-use type, both taxonomically and phylogenetically. Analysis of community turnover revealed the same distance-decay pattern observed for total prokaryotic communities (Rodrigues et al., 2013), indicating spatial biotic homogenization in pastures compared to forests. However, this result was more apparent taxonomically than phylogenetically. Similar to the local diversity increase observed in total prokaryotic communities, taxonomic and phylogenetic richness increased significantly in pasture soil (Mirza et al., 2020). Compositional comparison of sequenced clones have revealed that Deltaproteobacteria, uncultured Spirochaetes, Verrucomicrobia, and Archaea are favored in pastures while Cyanobacteria, several Firmicutes, and an uncultured Archaea are found exclusively in forests. While the finding of strong compositional differences is interesting, the inability to annotate below the phylum-level in this study limits interpretation (Mirza et al., 2014). Co-occurrence networks built from Rondônian forest and pasture microbiomes have further suggested an important role of diazotrophic taxa in pasture communities (Khan et al., 2019). A survey conducted in the Tapajós National Forest in Pará compared total N fixation-associated gene sequence counts from metagenomes across forests and pastures, and found a significant association with pasture soils across both the wet and dry season, which is in agreement with findings from Rondônia (Pedrinho et al., 2020). This was also bolstered by *nifH* gene amplification via qPCR, which reflected significant increases in pasture. Gene abundance has also been

measured at significantly higher concentrations in corn/soy cropping systems 2 years following forest conversion, compared to primary forests (Merloti et al., 2019).

However, quantification of *nifH* genes by Lammel et al. (2015b) and Paula et al. (2014) via GeoChip profiling conversely inferred significantly larger diazotrophic communities in primary forest compared to pasture. The cause for disagreement between groups of studies is not readily apparent but may be due to regional heterogeneity, the impact of grazing intensity on nutrient status and belowground C allocation by forage grass roots, or operational factors such as taxonomic coverage of the primers selected. Furthermore, diazotrophy is phylogenetically widespread across prokaryotes (Gaby and Buckley, 2014), and presence of taxa capable of ANF does not imply activity. The future inclusion of rate measurements to support molecular data is imperative in order to more conclusively understand diazotrophic response to land-use change.

6.2 Nitrification, denitrification, and N oxide flux

Nitrification, a multistep reaction whereby NH_4^+ is converted to NO_3^- (Fig. 6), is crucial in the overall N cycle of terrestrial ecosystems. This process impacts N oxide emissions, leaching potential, and preferential nutrient availability to plants and microbes (Pajares and Bohannan, 2016). Nitrification is mediated by chemolithoautrophic ammonia oxidizers of both the archaeal (AOA) and bacterial (AOB) domains, nitrite-oxidizing bacteria, and heterotrophic bacteria and fungi that can utilize organic N as a substrate (Zhu et al., 2014). A study of N cycling rates across forest and pasture chronosequences in Rondônia, Brazil, measured a decline in NO_3^- pool sizes with forest-to-pasture conversion, which typically coincided with consistently reduced net nitrification rates. Gross rates of nitrification were subsequently shown to decline with pasture conversion (Neill et al., 1996; Neill et al., 1997b). Furthermore, these patterns appear stable across both dry and wet seasons.

More than a decade later, a comprehensive survey of ammonia oxidizers with pasture conversion at ARMO sites in Rondônia revealed a significant decrease (>10-fold) in Thaumarchaeal *amoA* gene copy numbers, as discussed previously (Hamaoui et al., 2016). This trend was present irrespective of pasture age since conversion, and the results are consistent with earlier findings at ARMO sites using GeoChip 4.0 (Paula et al., 2014). Intriguingly, AOB were not detectable in this study, even with the use of

several primer sets. This may be due to the low pH in these environments or stronger inhibition of AOB communities by brachialactone production (Hamaoui et al., 2016; Hatzenpichler, 2012; Subbarao et al., 2015). Overall, the community structure of Thaumarchaeal ammonia oxidizers was significantly dissimilar between land-use types, and compositional analysis revealed the most drastic shift to be an almost complete removal of taxa from the genus *Nitrosotalea* in pastures. While the driving mechanism of *Nitrosotalea* loss is unknown, it may have important implications for depressed rates of nitrification (Shen et al., 2013). In contrast to the above study, a significant increase in absolute abundance of AOA was observed in 25-year-old pastures near Sinop, Mato Grosso (Lammel et al., 2015a). However, in Lammel et al. (2015a), AOB were detected in pasture soils, but there abundance was approximately half that measured in forest soils. In addition, NO_3^- pool size was significantly lower in pastures compared to forests, consistent with nitrification inhibition by brachialactone and/or overall N limitation. It is possible that differential abundance trends in Hamaoui et al. (2016) and Lammel et al. (2015a) are due to variable selection pressures across AOA and AOB community members with pasture conversion, but the latter study did not measure compositional differences. Earlier analysis of total archaeal *amoA* gene diversity from primary forest and pasture in Benjamin Constant found slight reductions in diversity with pasture conversion, but increases in richness (Navarrete et al., 2011). In addition, no reduction in NO_3^- pool size was observed. Forage species present in these pastures were not specified, so it is uncertain whether nitrification inhibition occurs in these soils. If pastures are overgrazed, depression in labile subsurface C availability may also stimulate nitrification by decreasing N immobilization in microbial biomass (Neill et al., 1999). Further, the potential role of heterotrophic nitrification in NO_3^- production is unknown.

Nitrous oxide (N_2O) is a potent greenhouse gas with 300 times the warming potential of carbon dioxide over a 100-year period (Forster et al., 2007; UNEP, 2013). A meta-analysis of N_2O flux studies throughout the Amazon has revealed a consistent pattern: young pasture soils (<10 years) may increase slightly in annual emissions compared to forests (median 2.52 kg N ha^{-1} versus 2.42 kg N ha^{-1}), but older pastures show drastically reduced emissions (median 0.9 kg N ha^{-1}) that in some cases act as a slight sink (Meurer et al., 2016). Further, the productivity status of pastures appears to influence N_2O flux, with degraded pastures emitting less annually than active pastures, likely as a result of ecosystem N depletion (Verchot et al., 1999).

N_2O is yielded through the reduction of NO_3^- or NO_2^- (Fig. 6), which may be performed as an incomplete anaerobic respiration reaction by heterotrophic denitrifiers or autotrophic nitrifiers (Bateman and Baggs, 2005; Patureau et al., 2000; Wrage et al., 2001). A gene-flux paired study in Mato Grosso found that nitrite reductase (*nirK*) and nitrous oxide reductase (*nosZ*) absolute gene abundances decreased in a 25-year-old pasture compared to a forest. An alternate nitrite reductase gene, *nirS*, was also measured in this study, and conversely showed a two-fold increase in pasture. While there is no clear understanding of divergent trends in *nirK*/*nirS* abundance given they perform the same function, *nosZ* and *nirK* counts may agree due to genomic co-occurrence (Jones et al., 2008). N_2O flux measurements agreed with the meta-analysis discussed above (Meurer et al., 2016) both in trend and rate magnitude; emissions were roughly eight-fold higher in the forest than pasture. Further, the *nosZ* (clade I) gene count was a decent predictor of N_2O flux ($R = 0.61$, $P < 0.003$). Unsurprisingly, soil water content and NO_3^- concentration were also important physicochemical predictors. Using GeoChip profiling, Paula et al. (2014) found no significant differentiation in *nirK* or *nosZ* gene abundance in pastures compared to forests, but did identify an overall association of denitrification genes in forest soils. Additionally, co-occurrence networks by Khan et al. (2019) suggested a greater importance of denitrification in Rondônian forests compared to pastures.

In a quantitative analysis of N-cycling communities, Pedrinho et al. (2020) conversely identified significant increases in absolute abundance of *nirK* (~three-fold) and *nosZ* (~two to three-fold) genes in pastures compared to forests, with consistent wet- and dry-season trends. Metagenomic read annotation reflected a significant increase in total denitrification-related genes in pastures during the dry season, but no difference during the wet season. The pasture surveyed in this study was approximately 13 years old, so although N_2O flux was not measured, trends from the meta-analysis suggest that emissions should be reduced compared to forests (Meurer et al., 2016). The genetic potential to contribute to denitrification is phylogenetically widespread (Chen et al., 2014; Shoun et al., 1992; Wei et al., 2015), so it may be that increases in *nirK* and *nosZ* genes are co-occurring with microbes that have an increased abundance in pastures due to an alternate set of conditions.

Nitric oxide (NO) is another biotically and abiotically produced gas that impacts ozone concentration in the atmosphere. It may be produced as a "leaky pipe" intermediate of nitrification, denitrification, or physicochemical

processes (Pilegaard, 2013). Data on NO flux in the Amazon are limited, but one study found that similar to N_2O, annual NO production was considerably higher in primary forest ($1.5\,kg\,N\,ha^{-1}\,year^{-1}$) compared to pasture ($0.6\,kg\,N\,ha^{-1}\,year^{-1}$; Verchot et al., 1999). *nirK/S* genes catalyze the production of NO, but it is unclear how strong of a predictor their abundance may be for emission rates, and to the authors' knowledge, no studies related to land-use change in the Amazon have investigated this. Further molecular work paired with flux measurements is required to understand NO flux through the soil and atmosphere in relation to land-use change. Additionally, while Pedrinho et al. (2020) reported significant compositional shifts in N-cycling taxa with pasture conversion, no specific analyses have been conducted to explore diversity or compositional changes in communities capable of contributing to denitrification processes. This may be a valuable line of inquiry for future studies.

7. Conversion by fire

The cumulative impact of land-use change on the activity, abundance, and community composition of soil microbes is likely impacted by the process of land-use conversion itself, most commonly through slash-and-burn clearing. This is important for consideration in the Amazon, where slash-and-burn practices occur on a range of scales, from large fires for pasture establishment (the primary land-use conversion type addressed in this chapter), to smaller-scale subsistence farming practices called "shifting cultivation". Forest burn in the BLA corresponds with total rates of deforestation, which has likely been intensified by climate change-related warming and drought over the past decades, releasing approximately 1600 kg CO_2 ton dry biomass^{-1} burned on average (Barkhordarian et al., 2017; Cochrane and Laurance, 2008; Silva et al., 2021; van Marle et al., 2017). Fire alters above- and belowground plant communities, and to varying degrees may impact soil textural and structural properties, biogeochemical pools, nutrient ratios, soil organic matter quality, and live microbial abundance, depending on heat intensity, preexisting organic matter content, or soil texture and bulk density (Butler et al., 2017; Cochrane and Laurance, 2008; Mataix-Solera et al., 2009). Within 1 day to several months, direct sterilization may reduce microbial biomass C significantly. Previous studies have indicated a biomass reduction of 64% and 74% for soil depths to 5 or 10 cm, respectively, following slash-and-burn clearing (Luizao et al., 1992;

Prieto-Fernández et al., 1998). Overall, bacteria have typically been found to be more resistant to the effects of fire than fungi in both temperate and tropical forests. Fungal sensitivity may be attributed to their broad hyphal networks (Aguilar-Fernandez et al., 2009; Barraclough and Olsson, 2018; Rashid et al., 1997); however, studies have found that microbial biomass has been negatively impacted for several years post-burn (Prieto-Fernández et al., 1998). Also impacted post-burn are biomass C (Luizao et al., 1992), spore diversity, and viability (Aguilar-Fernandez et al., 2009), which eventually return to pre-burn values or increase, suggesting the potential for rapid rebound of populations.

Aside from direct heat effects, communities are likely to be indirectly impacted by the availability of easily metabolized C and N compounds. An initial flush of surface layer (0–10 cm) extractable C and N compounds immediately following forest burn commonly coincides with microbial biomass losses through heat sterilization; in the medium-term (2 months to several years following burn), surface soil concentrations of organic matter are typically similar to, or lower than, unburned forest stands (Navarrete et al., 2015a; Neill et al., 1995; Prieto-Fernández et al., 1998). Additionally, fire is likely to lower the ratio of available C:N (Bomfim et al., 2020; Prieto-Fernández et al., 1998) given the volatility of C compounds. This shift in C and N availability may impact the composition and diversity of recovering microbial communities, particularly if burns are repeated (Zarin et al., 2005). Organic matter in soil may also be changed to a "pyromorphic" humus, negatively impacting its susceptibility to microbial degradation and water-holding properties (Gonzalez-Perez et al., 2004). Microbial communities of tropical forest soils may also be impacted by post-fire P (a limiting nutrient in tropical forests) availability, which has a high volatilization temperature (Butler et al., 2017), meaning it should be enriched in post-fire ash relative to pre-fire bulk surface soil. The availability of other crucial cations should also be enhanced given that ash increases soil pH (Neill et al., 1999; Ribeiro Filho et al., 2015). In tropical systems, a large proportion of ecosystem nutrients (C, N, P, etc.) are stored in biomass rather than soil pools (Wan et al., 2002). While fire may initially release these nutrients, the replacement of biomass-dense forest stands with perennial bunchgrass means that a smaller quantity of nutrients can be immobilized as plant biomass per unit area, and negatively charged inorganic molecules are particularly at risk of leaching from soil over time, especially under heavy rainfall. Specific impacts of these post-burn nutrient shifts on soil microbial communities are largely unknown.

Surprisingly limited work has been done exploring the short-, medium-, and long-term impacts of controlled or uncontrolled forest burns on soil microbial community structure, either in tropical systems or otherwise. There appears to be a consensus across several studies that in the short- and medium-term, microbial diversity increases or stays the same, and that community composition shifts in association with changes in pool size of available soil nutrients, particularly C and/or N (Fontúrbel et al., 2012; Lucas-Borja et al., 2019; Navarrete et al., 2015a; Prendergast-Miller et al., 2017). In particular, Navarrete et al. (2015a) found that 2–4 months after slash-and-burn deforestation, prokaryotic alpha diversity (measured via Simpson index) increased significantly (~70%) at two of three surveyed sites in Mato Grosso, Brazil. Additionally, for copiotrophic taxa, such as Actinomycetales, an increase in richness and relative abundance following burn appeared to be related to N availability. The study also found a decrease in Planctomycetes, Chlamydiae, and Verrucomicrobia following slash-and burn. The latter finding is interesting given that Verrucomicrobia have been shown to increase in diversity once pastures are established (Ranjan et al., 2015), suggesting the ecological resilience of this group. Indeed, Verrucomicrobia appear to be adapted to a low concentrations of substrate, as would be the case post-burn (Noll et al., 2005). Shifts in favored taxa have been observed elsewhere as well, such as increased abundance of Firmicutes, some of which are capable of endospore formation, a robust survival tactic under unfavorable conditions (Ferrenberg et al., 2013; Lucas-Borja et al., 2019; Prendergast-Miller et al., 2017). This is consistent with many studies previously discussed, which found an increase in Firmicutes with pasture conversion (e.g., Rodrigues et al., 2013). In the northern Amazon region, a 16S rRNA gene-based community composition study following the fire preparation of a pasture site reflected lower species diversity and richness in comparison to surveyed primary forests (Melo et al., 2021); however, the functional consequence of this is unknown.

Shifts in microbial function as a result of slash-and-burn in the Amazon have been indicated in a few studies. Just months after fire conversion, genes related to protein metabolism decreased up to 30% in burned areas, while genes related to DNA metabolism increased in pasture plots in Mato Grosso (Navarrete et al., 2015a). The latter finding may serve as an indication of survival and maintenance of genetic material during periods of unfavorable conditions. In the Amazonia-Cerrado transition zone, a study on the effects of fire on seasonally-flooded forest soils indicated that rates of a key soil microbial process, ANF, were on average 24% lower in burned

compared to unburned surface soils (0–10 cm; Bomfim et al., 2020). However, variable frequency of burn does not appear to add significant effect to this difference, and rates below 10 cm are unaffected by burning of any frequency. The mechanism of control over decreased activity is the shift in ratio of C to other nutrients such as N and P (Bomfim et al., 2020). This is consistent with previous work, which determined the quantity and characteristics of soil C post-burn to be significant determinants of ecosystem function (Gonzalez-Perez et al., 2004; Prieto-Fernández et al., 1998). The ANF study also found that while activity rates scaled linearly with nutrient ratios in unburned forests, relationships were highly nonlinear in burned forests, (Bomfim et al., 2020) potentially indicating an additional unmeasured impact of forest fires on diazotrophic soil communities, ultimately affecting activity rates.

Limited knowledge of the role of fire on microbial communities in the Amazon Rainforest and along its transitional zones presents a serious gap in knowledge. As previously mentioned, fire in the Amazon has been increasing in recent decades and will likely continue to do so for several reasons (Cochrane and Laurance, 2008). First, forest-clearing activities, including pasture conversion and shifting cultivation practices present new vulnerabilities for unplanned fires at forest margins (Barlow et al., 2016; Cochrane, 2001; Cochrane and Schulze, 1999). Indeed, a recent analysis has spatially linked the outbreak of accidental forest fires to ongoing deforestation (MAAP, 2019). Second, forest clearing has a positive feedback effect on climate change-related shifts in the hydrologic cycle through the release of C to the atmosphere as well as a direct alteration of local and regional scale air moisture circulation patterns (Betts et al., 2009). Therefore, understanding soil microbial community response to Amazonian forest fires will be crucial in further elucidating the explanatory factors of long-term compositional and metabolic shifts of soil microbial communities in response to abrupt disturbance and long-term land-use change.

8. Secondary forest recovery

This chapter has focused primarily on the conversion of primary forest to cattle pasture in the Amazon, as this has been the most widespread cause of land-use change throughout the region. However, it is not uncommon for pastures to be abandoned within 5–15 years of establishment due to the loss of forage grass productivity (Asner et al., 2004). In the years following abandonment, secondary forests begin to form. At present, it is estimated

that approximately 30–50% of previously converted pastureland is in some stage of succession (Chazdon et al., 2009; Pacheco, 2012), a reality that raises important questions as to whether microbial communities of these secondary forests rebound to a similar state of taxonomic and functional diversity as primary forests. Furthermore, it is unknown what implications this has for the biogeochemical cycles that microbial communities in secondary forests mediate. Some studies have compared communities of primary forest and pasture to that of secondary forests, and many conclude that microbial diversity indices of secondary forest are more similar to primary forests than active pastures. Evidence related to functional recovery is more mixed, with results varying by the specific function considered. Table 2 summarizes these findings and includes relevant metadata from studies discussed throughout this section. Fig. 7 correspondingly provides the geographic locations of these studies.

8.1 Microbial composition and abundance in succession

Mycorrhizal populations are presumably essential in forest succession. They are crucial in successful seedling recruitment by providing vulnerable roots with nutrients, water, and pathogen protection (Igwe and Vannette, 2019; Nara, 2006; Ueki et al., 2018; Van Der Heijden, 2004; van der Heijden et al., 2016). In a study of AM fungal diversity on the Eastern Amazonia margin, species richness and spore abundance were indistinguishable between young, degraded-secondary forests and mature rainforests during the rainy season. Intriguingly, spore abundance and diversity were actually significantly higher in young secondary forests during the dry season (Reyes et al., 2019). Species composition was similarly more affected by seasonality than forest type or age, indicating that AMF are resilient members of the soil microbial community despite high levels of historic disturbance. A survey of forests in succession across several Brazilian biomes has demonstrated that plant species involved in early succession engage in dense rates of AM colonization, likely investing in fungal recruitment to maximize capacity for nutrient acquisition (Zangaro et al., 2012); this finding lends mechanistic support to the notion that AM fungal communities recover quickly with reforestation. Total fungal communities of secondary forests are also more similar to those of primary forests than pastures, but this similarity appears dependent on geographic distance from forests, potentially indicating that primary forests can act as species reservoirs for the recolonization of secondary forests in succession (Mueller et al., 2016). This result also suggests that

Table 2 Summary of microbial studies discussed in this chapter, investigating the impact of secondary forest recovery following primary forest to pasture conversion and abandonment in the Amazon.

LUS Effect Measured	Parameters Measured	Secondary Forest Age	Köppens Class Annual Temp, Precip	Soil Type	Location (s)	Findings (*=significant)	Citation
Div of bact and comm structural controls (soil - Phys/Chem prop.)	-T-RLFP cloning/seq of bact comm -Phys/Chem prop.	<5 yr 5-30yr	Af 25.7° C 2562mm	Incept	Benjamin Constant, Amazonas State, Brail	*Sfor become more similar (str and comp) to pfor w/succession age compared to other LUS	(1) da C Jesus et al. 2009
Comp and relative abund of the phylum Verrucomicrobia	-Verrucomicrobia -specific 16S gene comp -Phys/Chem prop.	10yr	Aw 25.5° C 2200mm	Kand	Fazenda Nova Vida (10°10′5″S and 62° 49′ 27″ W)	*Verrucomicrobia div higher in sfor (tax, but not phylo) *Absolute abund assoc w/C content *Comp str more similar to pfor than past	(2) Ranjan et al 2015
Div and comm str of archaeal domain	-PCR DGGE of 16S rRNA gene -clone library of *amoA* gene -Phys/Chem prop.	2yr 16yr	Af 25.7°C 2562mm	Incept	Benjamin Constant, near Solimões River, Amazonas state, BR	*Archaeal comms more similar in pfor and sfor than past or crop *Div of NH_3- oxidizing archaea lower in sfor vs pfor, past, or crop systems	(3) Navarrete et al. 2011
Func gene comp shifts with LUS change	-GeoChip4.0 gene probe -Phys/Chem prop.	13yr	Af 25.5° C 2200mm	Kand	Ariquemes, Rondônia (ARMO; 10° 10′18.71″S, 62° 47′15.67″W)	-Suggests incomplete funct recovery in sfor *High spatial turnover of gene profiles	(4) Paula et al. 2014
Abund and comm str of thaumarchaeal ammonia oxidizers	-qPCR of *amoA* gene -Pyroseq thaumarchaeal *amoA*, 16S	NR	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia (ARMO; 10° 10′18.71″S, 62° 47′15.67″W)	*Thaumarchaeal abund similar across pfor and sfor -Comm str is more similar to pfor than past	(5) Hamaoui et al. 2016
Whole comm div and func resp to soil conditions under land use change	-MG -Phys/Chem prop.	13-15 yrs	Am 26° C 2150mm	Ox	Tapajós National Forest, Pará, BR - 2°51'23.9'S, 54°57'28.4'W	*Tax div of sfors is similar to that of pfors rather than active past *Func div was higher than pfor, and more similar to pasts	(6) Pedrinho et al. 2019

Continued

Table 2 Summary of microbial studies discussed in this chapter, investigating the impact of secondary forest recovery following primary forest to pasture conversion and abandonment in the Amazon.—cont'd

LUS Effect Measured	Parameters Measured	Secondary Forest Age	Köppens Class Annual Temp, Precip	Soil Type	Location (s)	Findings (*=significant)	Citation
Div of whole fungal comm	-DGGE of 18S rRNA gene	NR	Af 25.7° C 2562mm	Incept	Benjamin Constant, Alto Solimões, Amazon State, BR	-Sfor comms more similar to pfor and agrofor sites than past	(7) Fracetto et al. 2013
AM fungi div	-Spore count -Spore taxonomy -Plant species	>20 yr (old) <20 yr (young)	Af 25.7° C 2562mm	Incept	Benjamin Constant, Alto Solimões, Amazon State	*Inc'd spore div/count for both young and old sfor *Comm comp differs between pfor and sfor	(8) Sturmer and Siqueira 2011
AM fungi div/ seasonality and soil prop relationship	-Spore count, -Species comp/div -Glomalin content	3-4yr (young) 6-8yr (mid) >120yr (mature)	Aw 2370mm	Typic Haplaustox	Alcântara county, Amazonia periphery, BR (2° 23′ 51″ S, 44° 24′ 16″ W)	*_Glomus_ and _Acaulospora_ dominate samples regardless of season -No difference in glomalin content (high % of SOC) *Seasonality more signif than successional age *Spore density higher in dry young-mid sfor compared to mature pfor	(9) Reyes et al. 2019
Fungal/ plant comm relationship	-Fungal rDNA comp -Plant _trnL_ comp	12yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	ARMO, Rondônia (ARMO; 10° 10′18.71″S, 62° 47′15.67″W)	*Comp differs across for types *Basidiomycota dec in sfor	(10) Mueller et al. 2014
Fungal comm/ distribution patterns across LUSs	-Fungal rDNA comp, rich	12yr 17yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia (ARMO; 10° 10′18.71″S, 62° 47′15.67″W)	*Variable rich and comp divergence compared to pfor -No clear trends in generalist vs specialist fungi	(11) Mueller et al. 2016

C cycling activity and SOC characterization along LUS chrono-sequence	- ß- glucosidase enzyme activity - Fourier-transform spectroscopy -POXC	12yr, 18yr	Af 25.5° C 2200mm	Kand	Ariquemes, Rondônia (ARMO; 10° 10′18.71″S, 62° 47′15.67″W)	*Characterization of SOC based on organic derivative and absolute (POXC) is very similar to pfor, but POXC as fraction of total C is similar to past * ß- glucosidase activity is similarly high to pfor	(12) Durrer et al. 2021
Relationship between CH_4 production and methanogen/troph comms	-CH_4 flux -amplicon seq, *pmoA* and *mcrA*	NR	-2200mm (Rond.) -2000mm (Tapa.)	-Kand (r/y pod-lat; Rond.) -Ultisols, Oxs, Incepts (Tapa.)	-Ariquemes, Rondônia -Tapajos National Forest, Pará	*CH_4 flux rates similar to pfor *Methanogen/troph rich and relative abund similar to pfor	(13) Meyer et al. 2020
Active methanotrophic comms	-SIP amplicon seq (methanotrophs and methanogens) -MG	NR	NR	NR	-Ariquemes, Rondônia -Tapajos National Forest, Pará	*Active comms more similar to pfor than past *methanotrophs more active than methanogens	(14) Kroeger et al. 2021
N-cycling comm comp and function	-MG -qPCR of N-cycling genes (*nifH*, *nirK*, *nosZ*) - Soil Phys/Chem	17yr	Am 26° C 2150mm	Ox	Belterra municipality, State of Pará, BR	*Comm tax and func str of N-cycling comms are distinct between pfor and sfor, -Div and rich are similar **nirK* and *nosZ* gene counts are higher in sfor	(15) Pedrinho et al. 2020
Viability, div, and efficiency of symbiotic (nodulating) diaz	-Nodulation density and efficiency of promiscuous legume	<5yr (young) >5yr (old)	Af 25.7° C 2562mm	Incept	Benjamin Constant, Alto Solimões, Amazon State, BR	*Nodulation number slightly higher in sfor compared to pfor -Similar strain efficiency	(16) Lima et al. 2009
Isolation of free-living diaz to determine div	-Isolation of culturable free-living diaz + protein profiling -nitrogenase activity	NR	Af 25.7° C 2562mm	NR	Benjamin Constant, Alto Solimões, Amazon State, BR	-Yielded a similarly low number of isolates as pfor, with moderate potential activity	(17) Silva et al. 2011

Continued

Table 2 Summary of microbial studies discussed in this chapter, investigating the impact of secondary forest recovery following primary forest to pasture conversion and abandonment in the Amazon.—cont'd

LUS Effect Measured	Parameters Measured	Secondary Forest Age	Köppens Class Annual Temp, Precip	Soil Type	Location (s)	Findings (*=significant)	Citation
Potential of symbiotic N_2 fixation in recovering forests	- $\delta^{15}N$ levels in forest leaf litter -Survey of legume species	2-25yr	Am 26.4° C 3000mm	Kaolinitic Ox (yellow latosol)	70km east of Manaus, central Amazonia, BR	*High density of N_2-fixing legumes assoc with low $\delta^{15}N$ in leaf litter in sfor but not pfor *No diff in trend over 25 yr of sfor succession	(18) Gehring et al. 2005
Potential of N_2 fixation in degraded pasture	-^{15}N tracer analysis between forage grass and early successional species (legume and non-legume)	Aband pasture	Aw 26.5° C 1800mm	Kaolinitic yellow latosols	Fazenda Vitória, Paragominas, Pará, BR	*Successional legume species may obtain 75% of N from symbiotic fixation, 27% of total across species -atmospheric N not detected in forage grass	(19) Davidson et al. 2018
Diaz comm div	-*nifH* clone seq -qPCR of *nifH* gene	10yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia (ARMO; 10° 10′18.71″S, 62° 47′15.67″W)	*Tax but not phylo distinct from pfor *More gene copies than pfor, but less than past *Firmicutes, alpha, and beta proteobacteria enriched in sfor	(20) Mirza et al. 2014
Distance-decay relationship of diaz comms	-*nifH* gene seq -soil Phys/Chem prop	12-17yr	Aw 25.5° C 2200mm	Kand (r/y pod-lat)	Ariquemes, Rondônia (ARMO; 10° 10′18.71″S, 62° 47′15.67″W)	*Tax rich and phylo div are similar to pfor, lower than past *Beta div (distance-decay) is higher than past, and similar to pfor	(21) Mirza et al. 2020

Abbreviations: Aband: Abandoned.**Abund:** abundance/ abundant**. Agrofor:** Agroforestry**. Al:** aluminum**. AM:** Arbuscular mycorrhizal. ***amoA*:** ammonia monooxygenase gene. **ARMO:** Amazon Rainforest Microbial Observatory**. Assoc:** associated**. Bact:** bacteria. **BR:** Brazil. **C:** carbon**. CH_4:** methane**. Comm:** community. **Comp:** composition. **Crop:** Agricultural cropping system. **Dec:** decrease. **Defor:** Deforested. **Diaz:** diazotrophic. **Diff:** difference. **Dist:** distance. **Div:** diversity/diverse**. Esp:** especially. **Func:** functional/function. **Inc:** increase**. Incept:** Inceptisol. **K:** potassium. **Kand:** Kandiudult. **LUS:** LUS systems**. *mcrA*:** methyl coenzyme M reductase gene**. MB:** microbial biomass. **Metab:** metabolism/metabolic.**MG:** Metagonomic profile (DNA-based). **MR:** microbial respiration. **N:** nitrogen**. NA:** Not applicable. ***nifH*:** nitrogenase reductase**. *nirK*:** nitrite reductase gene**. *nosZ*:** nitrous oxide reductase gene**. NP:** Not provided.**Oxisol:** Oxisol. **Past:** pasture**. PCR DGGE:** polymerase chain reaction denaturation gradient gel electrophoresis**. Pfor:** primary forest. **Phys/Chem prop:** Physicochemical properties**. *pmoA*:** particulate methane monooxygenase**. POXC:** permanganate oxidizable carbon**. Phylo:** phylogenomic/phylogenetic. **Precip:** precipitation. **Pyroseq:** pyrosequencing**. qPCR:** quantitative Polymerase Chain Reaction. **Resp:** response.**Rhiz:** rhizosphere. **Rich:** richness. **r/y pod-lat:** red-yellow podzolic latosol. **Sfor:** secondary forest**. Seq:** sequencing**. Signif:** significant. **SOC:** soil organic carbon**. SIP:** Stable Isotope Probe**. SOM:** soil organic matter**. Str:** structure/structural. **Tax:** tax/tax. **Temp:** Temperature**. T-RLFP:** terminal restriction length fragment polymorphism**. *trnL*:** chloroplast intron gene. **Ult:** ultisol.**Yr:** year/s. **16SrRNA:** prokaryotic ribosomal RNA gene (DNA-based)

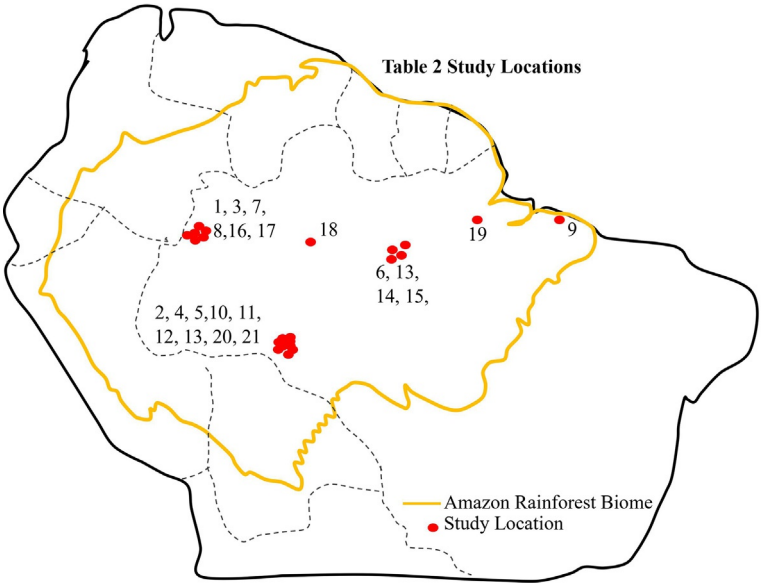

Fig. 7 Geographical distribution of studies presented in Table 2. Labels correspond to number in "Citation" column.

considering inter-sample distance at scales as large as several kilometers may be an important predictor of fungal composition.

Similarly, prokaryotic communities appear to respond to reforestation over time. Comparison of several secondary forests of varying age has shown greater similarity in community structure and composition between primary and older secondary forests (~5–30 years) compared to younger secondary forests (<5 years), indicating a trajectory to recovery (da C Jesus et al., 2009). This pattern has also been reflected in a narrower community scope: a survey of Verrucomicrobia using phylum-targeted amplification and sequencing revealed greater similarity between secondary and primary forest community structures compared to pasture, although diversity of taxa within the phylum was higher in secondary than primary forests (Ranjan et al., 2015). Additionally, targeting archaeal communities using PCR-DGGE has indicated greater similarity of primary forest communities with those of secondary forests, compared to pastures and cropping systems (Navarrete et al., 2011). A metagenomic-based analysis found greater taxonomic similarity between primary and secondary forest compared to pasture, but also discovered that the functional diversity of a ~14-year-old secondary forest, similar to pastures, was elevated in comparison to primary forest

(Pedrinho et al., 2019). Functional profiling using the GeoChip 4.0 showed greater similarity of overall functional gene richness and diversity between primary and secondary forests compared to pastures, but substantial differences were found in specific gene composition (Paula et al., 2014). The results of these studies may indicate that despite vegetational succession, legacy effects of pasture on soil conditions, such as nutrient status, may present a lag in the recovery of soil functions compared to taxonomic representation.

8.2 Microbial function in succession

Studies comparing microbial-mediated C degradation across primary forest, pasture, and secondary forest have been fairly limited and have mixed results. One study across a land-use chronosequence at ARMO, State of Rondônia, Brazil, analyzed C dynamics in 13–18-year-old secondary forests that were abandoned after 7–10 years of pasture use. The study found that the organic C profiles (quantity and chemical composition) of secondary forest soil closely resemble that of primary forests, with concomitant increases in C-cycling enzyme (β-glucosidase) activity (Durrer et al., 2021); this pattern is perhaps intuitive because the plant community and detrital substrate of secondary forest is much more similar to original forests than pastures filled with exotic grasses. The interrelationship of CH_4-C emissions and methane-cycling microbial functional groups with forest recovery is of distinct interest. In a recent study of methane-cycling communities in Rondônia, the richness and relative abundance of methanogens in secondary forest showed a significant decline relative to pasture, while the richness and relative abundance of methanotrophs showed a significant increase (Meyer et al., 2020). Active methanotrophic communities of secondary forests are also more structurally comparable to primary forests than pastures (Kroeger et al., 2021). These findings are supported by flux measurements that identified secondary forest as a weak sink ($-10.2 \pm 35.7\,\mu g\,CH_4\,m^{-2}\,day^{-1}$) compared to pasture, which typically acts as a source (Meyer et al., 2020). A similar conclusion was reached in a timeseries land-use gradient study, namely, secondary forests (as well as degraded pastures) were found to be a year-round weak net sink of methane (Verchot et al., 2000). However, in the latter study, seasonal patterns of methane flux differed substantially across all land-use types, indicating some persisting differences in methane-cycling microbial communities, and potentially soil physicochemical conditions.

As discussed previously, pastures may become N limited with age, particularly if land management is unsustainable. It stands to reason that following pasture abandonment, recuperation of N is likely to be an important aspect of reforestation, particularly in early stages (Davidson et al., 2007). Elucidating shifts in N-cycling microbial community members in secondary forests compared to primary forests and pastures is likely to improve our understanding of how N flux rates and pool sizes change with forest succession. Evidence from multiple studies would suggest that, with secondary forest succession, the abundance of diazotrophs decreases in comparison to pasture, contracting toward primary forest levels (Mirza et al., 2014; Pedrinho et al., 2020). Community taxonomic and phylogenetic diversity at the local scale comparably decreases, but turnover at the landscape scale increases in secondary forests (Mirza et al., 2020; Silva et al., 2011), indicating a reversal of the biotic homogenization effect of pasture establishment identified by Rodrigues et al. (2013). Additionally, compositional structure of diazotrophs is highly similar between primary and secondary forests compared to distinct pasture community structure (Mirza et al., 2020). A study that used GeoChip profiling similarly found that the trend of nitrogen fixer abundance of secondary forests became more similar to that of primary forests (Paula et al., 2014). Interestingly, study of SNF potential suggests this may be an important process as forests recover (Lima et al., 2009). A claybox mesocosm experiment in abandoned pastures using a ^{15}N tracer revealed that early secondary forest legume species may obtain 75% of biomass N content from SNF- diazotrophs (Davidson et al., 2000). Survey of legume density in forests of central Amazonia has shown that in secondary forests, depression of leaf litter $\delta^{15}N$ is positively correlated with higher legume density compared to primary forests (Gehring et al., 2005). This suggests higher rates of SNF in secondary forests than in primary forests. The study further concluded that this trend is consistent in successional forests spanning multiple decades in age. Taken together, this indicates a potentially divergent role of associative and free-living versus symbiotic N_2 fixers in recovering secondary forests, warranting further study.

Ammonia oxidizers of the Thaumarchaeota, an archaeal phylum, reflect one of the most dramatic drop-offs of any group in converted pasture soils. An ARMO-based analysis demonstrated community revival with secondary forest succession: the absolute abundance of an *amoA* marker gene in secondary forest soil was akin to that of primary forests, and approximately an order of magnitude higher than in pastures. While distinct, ammonia-oxidizing archaeal community structure of secondary forests showed greater

similarity to primary forest than pastures (Hamaoui et al., 2016). Although gross and net rates of N mineralization and nitrification were not directly measured in this study, concentrations of NH_4^+ ($\sim$5.5 μg-N g^{-1} soil) and NO_3^- ($\sim$3.7 μg-N g^{-1} soil) were nearly identical in primary and secondary forests, compared to much higher NH_4^+ ($\sim$14 μg-N g^{-1} soil) and virtually no NO_3^- present in pastures. These results suggest recovery of this microbial functional group is concomitant with restoration of the environmental processes they mediate. The results of this study were supported by previous GeoChip profiling, which showed that nitrification genes were significantly associated with primary and secondary forest compared to pasture (Paula et al., 2014). In contrast, a PCR clone-based study in Benjamin Constant found considerable differentiation in archaeal *amoA*-based community structure between primary and secondary forest types, with primary communities more similar to those of pastures (Navarrete et al., 2011). Additionally, richness and diversity metrics of *amoA* communities were appreciably lower in secondary forests compared to primary forests or pastures. This variability across studies may be explained in part by large differences in trends of inorganic N pool sizes in opposing land-use types: While NH_4^+ concentrations did increase in pastures relative to primary forest, concentrations of NH_4^+ in secondary forests were significantly lower than both. Further, no difference was observed in NO_3^- concentrations across land-use types. Of course, factors like secondary forest age and N limitation status at the time of abandonment certainly play a role in the trajectory of N-cycling as forests regrow.

A comprehensive analysis of all N-cycling microbes as interpreted from metagenomic data suggests that taxonomic and functional community structure shifts with pasture abandonment but remains distinct from primary forests (Pedrinho et al., 2020). Patterns of diversity in the N-cycling community showed inconsistent trends: taxonomically, primary and secondary forests were similar compared to elevated diversity in pastures, but in terms of functional diversity (and abundance of reads relative to whole metagenomes), secondary forests were more similar to pastures. It appears that, while secondary forest N-cycling communities do trend toward recovery (i.e., a primary forest-like state), initial persistent N limitation remains, potentially for several decades. This is reflected in metrics of foliar N, litterfall mass to N ratio, NO_3^- concentration, and N_2O production across primary forests, active/degraded pastures, and secondary forests (Davidson et al., 2007; Verchot et al., 1999). N_2O emissions from secondary forest in particular appear to have intermediary rates between primary forests and pastures (Verchot et al., 1999). Overall, the recovery of N-cycling

microbial groups is likely dependent on the degree of N limitation imposed by agricultural use, and secondary forest age is likely an important consideration when assessing recovery status related to N cycling.

More broadly, land-use history and intensity may impact many long-term aspects of reforestation such as rate of regrowth, forest density, and soil C stocks (Uhl et al., 1988; Zarin et al., 2005). Studies investigating the response of soil microbial communities to pasture abandonment and reforestation in the Amazon are sparse, and often lack a process-based measurement. Future research should focus on assessing the role of land-use history, including native forest conditions, land management decisions, and conversion/abandonment timelines (Fearnside and Guimarães, 1996; Zarin et al., 2005) on shaping the composition and function of the soil microbial community in secondary forests.

9. Conclusions

9.1 Considering the future of the Amazon

Concerns over not only biodiversity loss, but also contributions to climate change-related warming with deforestation in the Amazon Rainforest has helped increase public awareness of its global importance (Cerri et al., 2018). With climate change, it has become clear that more research is needed to understand how the Amazon Rainforest cycles and stores carbon. The complex role microbes play in this ecological function is still poorly understood and should be an essential focus of future microbial research in order to increase their representation in ecosystem models. Despite concerns, Amazon Rainforest losses have been increasing over the past ~5–6 years (Fig. 1A; INPE, 2020). While the drivers of Amazon Rainforest losses are not yet apparent, clearing of primary forest appears to be disproportionately more likely in small forest fragments compared to larger forest fragments (Hansen et al., 2020). Conservation efforts should therefore be focused on these larger contiguous fragments of forest. Ongoing fragmentation also indicates that further work is needed to understand the impact of edge-effects on soil microbial community diversity and function, since at present, this is a severely understudied aspect of microbial ecology. Recent analysis of forest loss in the Brazilian Amazon concluded that secondary rather than primary forests are now the dominant type being cleared, accounting for 72% of total deforestation as of 2014 (Wang et al., 2020), with over 90% of re-cleared land again converted to cattle pasture (Tyukavina et al., 2017). It is imperative that future studies—especially those focused on young pastures—take into account and assess the effect

of complex land-use histories that may include multiple forest/pasture cycles. Not only will this likely begin to explain variation in the data, but it also presents a unique opportunity to determine the extent to which soil microbiomes recover their community assembly when the land use shifts. Additionally, a recent effort toward grazing intensification in order to slow new deforestation (Barbosa et al., 2015) brings into question the response of soil microbes, both compositionally and functionally, to variable grazing pressures.

9.2 The complexity of microbial communities in response to land-use change

Attention to microbiomes of tropical forests, particularly the Amazon, has only gathered momentum in the past 15 years, fueled by our concerns over continued forest loss and degradation, and by a poor understanding of the role microbial diversity and function play in these vital ecosystems. A complex interaction of factors shapes soil microbial community response to land-use change in the Amazon, as has been discussed throughout this chapter. Fig. 8 attempts to conceptualize these interactions, but is by no means exhaustive. Land-use change factors (such as initial slash-and-burn clearing and changes in aboveground vegetation with pasture reseeding), and land management (including grazing practices, controlled burns, and abandonment) impact the microbiome directly and indirectly through complex feedbacks on soil physicochemical conditions. These changing conditions influence several aspects of the soil microbial community including abundance, compositional structure, and taxonomic, phylogenetic, and functional diversity.

This chapter has discussed in detail what is currently known of microbial community response to land-use change in the Amazon Rainforest and has put this in the context of shifts in important biogeochemical cycles such as C and N. However, there are still vast gaps in the understanding of regional variability in microbial community response, how environmental and management conditions shape these responses, and how shifts in community composition and structure relate to their environmental function and the biogeochemical cycles they mediate. Henceforth, employing computational approaches to better utilize the vast quantities of data generated through techniques such as metagenomics will hopefully impart a greater understanding of the ecological role microbial communities assume in tropical soils.

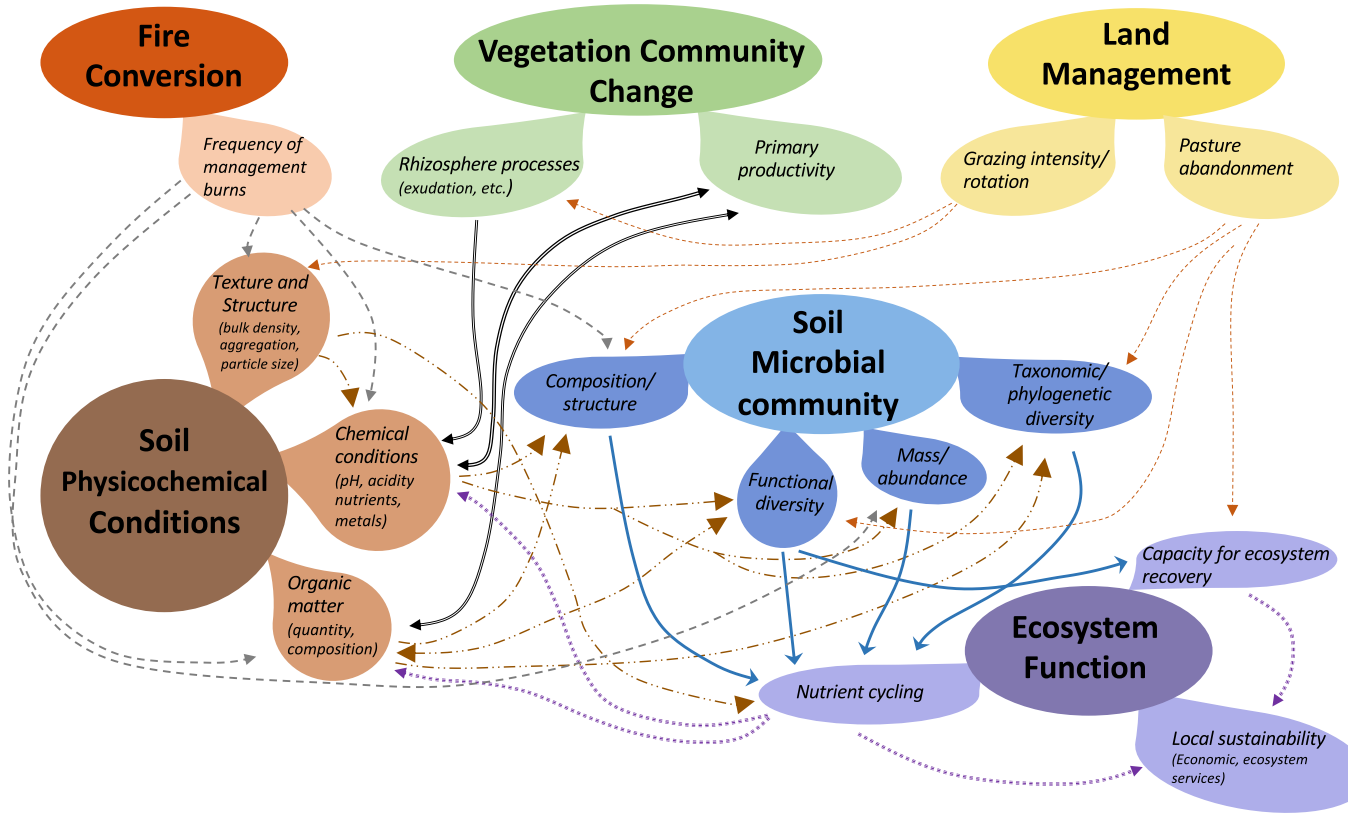

Fig. 8 Conceptual diagram of forest-to-pasture land-use disturbance in the Amazon. Changes in the plant community, use of fire for conversion and maintenance of pasture, and management vs. abandonment/reforestation influence a complex array of interactions between the soil environment, soil microbial communities, and ecosystem function. Interactions are direct, indirect, and may be two-way. Arrows included are based on causative or associative studies discussed throughout the chapter, but the diagram is not an exhaustive depiction of all ecological interactions. Arrow style is determined by the causative factor: Fire conversion—gray dashed; Vegetation community change—black double line; Land management—orange dots; Soil physicochemical conditions—brown dash/dot; Soil microbial community—blue solid; Ecosystem function—purple square dot.

Acknowledgment

The Soil Ecogenomics Laboratory received financial support from the National Science Foundation—Dimensions of Biodiversity (DEB 14422214) and the U.S. Department of Agriculture—NIFA (Award # 2009-35319-05186). This work was supported the U.S. Department of Energy Joint Genome Institute, a DOE Office of Science User Facility, supported by the Office of Science of the U.S. Department of Energy under contract DE-AC02-05CH11231. Support is also acknowledged through the USDA NIFA Pre-doctoral Fellowship to RD (Award No. 2019-67011-29554).

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