

CONSISTENT BACTERIAL RESPONSES TO LAND USE CHANGE ACROSS THE
TROPICS

by

IAN AB PETERSEN

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Student: Ian AB Petersen

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This thesis has been accepted and approved in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology by:

Brendan Bohannon Chairperson

and

Janet Woodruff-Borden Vice Provost and Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School.

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THESIS ABSTRACT

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Bacteria are a major component of global diversity and are involved in most terrestrial biogeochemical processes. Despite their importance, little is known about the response of bacteria to human-induced environmental change. Understanding the response to land use change is pressing for tropical rainforests, which are being altered rapidly. Here, we conduct a meta-analysis spanning the major tropical rainforest regions to ask whether there are consistent responses of bacterial communities to tropical rainforest conversion. Remarkably, we find commonalities despite wide variation in agricultural practices and research methodology. These responses include changes in abundance of phyla; decreases in Acidobacteria and Proteobacteria and increases in Actinobacteria, Chloroflexi and Firmicutes. We also find alpha diversity (at single soil core scale), consistently increases with conversion. These consistent responses suggest common features such as slash-and-burn tactics have the potential to alter bacterial community composition and diversity belowground.

This thesis includes previously unpublished, co-authored material.

CURRICULUM VITAE

NAME OF AUTHOR: IAN AB PETERSEEN

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
Lewis & Clark College, Portland

DEGREES AWARDED:

Master of Science, Biology, 2019, University of Oregon
Bachelor of Arts, Biology, 2013, Lewis & Clark College

PROFESSIONAL EXPERIENCE:

Teaching Assistant, Department of Biology, University of Oregon, Eugene,
Oregon, 2016-2019

Laboratory Technician, Center for Life in Extreme Environments (CLEE),
Portland State University, Portland, Oregon, 2014-2016

GRANTS, AWARDS, AND HONORS:

Graduate Fellowship, University of Oregon Biology Department, 2016 - 2019

Dean's Recruiting Fellowship, University of Oregon, 2016

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CHAPTER I

INTRODUCTION

Tropical rainforests are declining faster than any other ecosystem primarily due mostly due to agricultural expansion. From 1980 to 2012, approximately 1.3 million km² of tropical rainforest were cleared for agriculture, an area the size of France, Spain and the UK combined (Gibbs et al., 2010; Hansen et al., 2013). This conversion is concerning because it threatens ecosystem functions (DeFries, Field, Fung, Collatz, & Bounoua, 1999; Verchot, Davidson, Cattânio, & Ackerman, 2000) and leads to decreases biodiversity in an ecosystem that is home to >50% of terrestrial plant and animal species (Gardner et al., 2009).

Across the tropics, forest-to-agriculture conversion occurs through a similar mechanism, slash-and-burn, but differs in eventual agricultural characteristics. In slash-and-burn, valuable trees are removed for lumber and the remaining vegetation is burned to clear the land for agricultural use. Following slash-and-burn, the primary form of agriculture differs by region. Oil palm plantations are common in southeast Asia (Koh & Wilcove, 2008), beef cattle pastures or soybean plantations are common in the Amazon (Morton et al., 2006) and Congo Basin agriculture tends to be comprised of small scale subsistence farming of plantain or manioc (Sunderlin et al., 2000; Zhang, Justice, Jiang, Brunner, & Wilkie, 2006). Duration of agricultural use also varies by region, from one-three years for plantations in the Congo (Zhang, Justice, & Desanker, 2002) to decades of continual use in southeast Asia and the Amazon (Rodrigues et al., 2013; Tripathi et al., 2016).

Research on the impact of forest to agricultural conversion has largely focused on assessing the impact to plant and animal communities (Banks, Sandvik, & Keesecker, 2009; Bernard, Fjeldså, & Mohamed, 2009; Gibson et al., 2011; Newbold et al., 2015; Perfecto & Snelling, 1995), but there is growing interest in the effect of land use change on soil microbial communities (for example see, Rodrigues et al., 2013).

There has not yet been an effort to quantitatively ask whether responses are consistent. In chapter II, I describe a co-authored study in which we ask whether there are

commonalities in the response of below ground bacterial communities to land use conversion. To answer this question, we conducted a meta-analysis that includes studies with pan-tropical representation and with wide variation in agricultural characteristics and research methodology. Despite this variation, we identify consistent changes in the diversity and composition of belowground bacterial communities. These consistent responses suggest that, while there is great diversity in agricultural practices across the tropics, common features such as the use of slash-and-burn tactics have the potential to alter bacterial community composition and diversity belowground.

CHAPTER II

PAN-TROPICAL META-ANALYSIS OF BACTERIAL RESPONSE TO LAND USE CHANGE

This chapter includes co-authored material. The design was developed through collaboration between Dr. Brendan Bohannon, Dr. Kyle Meyer and myself. I conducted the literature search, compiled the data, performed the meta-analysis and wrote the text. Dr. Brendan Bohannon and Dr. Kyle Meyer contributed to manuscript revisions and contributed to idea development.

Introduction

There is growing recognition of the importance of understanding the response of bacterial communities to land use change. Soil bacteria mediate most biogeochemical cycles (Madsen, 2011) and comprise the majority of global biodiversity (Hug et al., 2016). When ecosystems undergo conversion, such as from forest to agriculture, biochemical cycles are often profoundly altered (DeFries et al., 1999; Neill et al., 1997, 2005; Verchot et al., 2000) and the diversity of plant and animal communities can decrease, along with changes in species composition (Banks et al., 2009; Bernard et al., 2009; Gardner et al., 2009; Gibson et al., 2011; Newbold et al., 2015; Perfecto & Snelling, 1995). No ecosystem type is experiencing conversion at a faster rate than tropical rainforests (Dirzo & Raven, 2003), which are declining primarily due to agricultural expansion (De Moraes, Volkoff, Cerri, & Bernoux, 1996).

There are a growing number of studies on the effect of land use change on belowground microbial communities in the tropics. We took advantage of this growing literature to ask whether there are commonalities across studies in the response of belowground microbial communities to ecosystem conversion. Specifically, we conducted a meta-analysis on the effects of forest to agriculture conversion on belowground bacterial communities and soil chemical properties across the world's three largest tropical rainforests (the Amazon Basin, the Congo Basin and southeast Asia). While there is great diversity in agricultural characteristics across the tropics, consistent patterns in bacterial response should nonetheless emerge if community change is driven

by common aspects of ecosystem conversion, such as slash-and-burn tactics. Despite regional differences in agricultural practices, and a diversity of research methodologies across studies, we observed consistent changes in diversity and phylum level composition.

Methods

We conducted a literature search on Web of Science and Google Scholar on the 23 January 2019. Search terms included: forest conversion bacteria, forest conversion bacterial and deforestation microbial. Titles and abstracts of articles matching our search terms were then screened for studies that directly compare soil samples from primary tropical rainforest with proximal agricultural sites, analyze metabarcode or metagenome sequences and report at least one diversity metric, composition at the phylum level and soil chemical characteristics. The literature search workflow is presented in Figure 1.

Following identification, means (X), standard deviations (SDs), and sample sizes (n) were extracted from the papers. If not reported, these statistics were derived from other metrics; standard error, 95% confidence interval, or diversity metrics and composition were derived and summarized from OTU tables using the vegan package in R 3.4.4. The meta-analysis was then conducted following Borenstein *et al.* (2009). Briefly, for each study a response ratio was determined for diversity, phylum-level relative abundance and soil chemical factors using the following equation

$$rr_i = \ln \left(x_{fi} / x_{ai} \right)$$

Where for study i , the means of forest and agricultural samples are represented respectively by x_{fi} and x_{ai} . To assess responses across all studies and a weighting value (w) was calculated.

$$w_i = 1 / var_{rr_i}$$

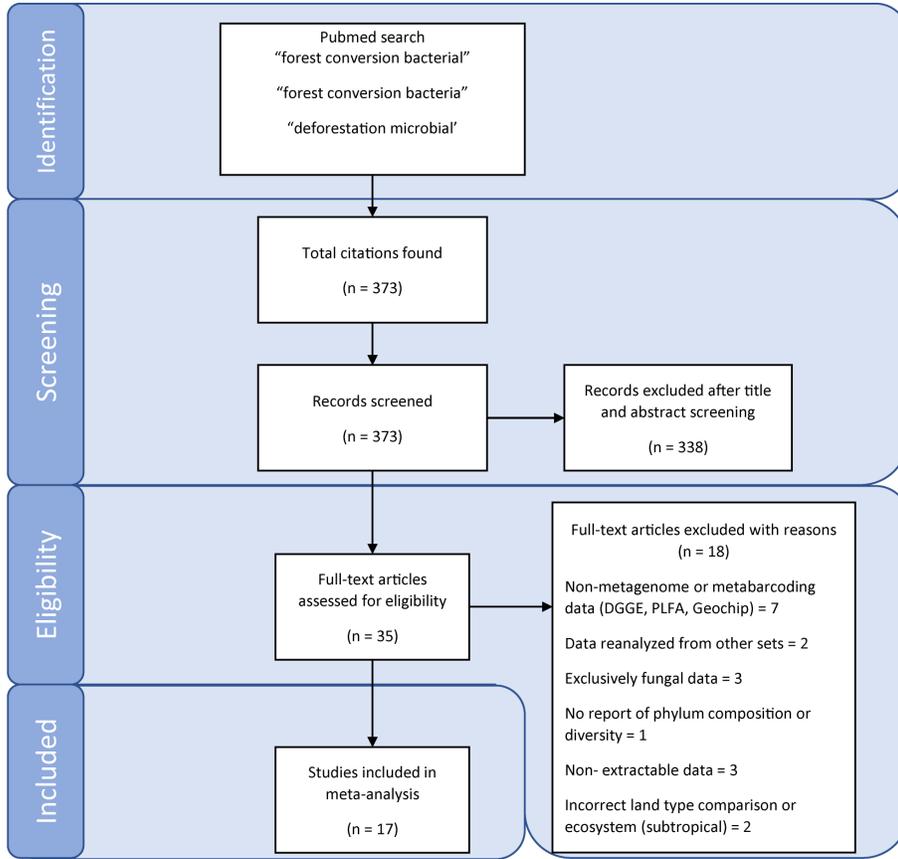


Figure 1: Flow diagram for the selection of manuscripts.

The summary response ratio (rr_w) was then calculated by averaging individual response ratios and weighting values.

$$rr_w = \frac{\sum_{j=1}^i w_i * rr_i}{\sum_{j=1}^i w_i}$$

To determine if the summary response ratio was significantly different from zero, we then conducted two tailed t-tests ($\alpha = 0.05$).

For phyla that we found to have a significant response, we then attempted to examine the consistency of response at finer taxonomic scales (order, class) using findings reported in the published papers or by deriving information from the underlying OTU tables.

Results

Our literature search identified seventeen studies (Table 1), with representation from all three major rainforests (Figure 2). A diverse set of agriculture types were represented, including cattle pasture (predominantly in the Amazon), oil palm plantation (exclusively in southeast Asia) and banana/manioc plantation in the Congo basin (Table 1). In addition to a diversity of study systems, a variety of sampling techniques were used; with soil cores collected along transects, quadrats or nested sampling schemes and sequencing of samples done individually or as pooled samples.

The V3 and/or the V4 region of 16S rRNA gene was sequenced in all studies using 454 pyrosequencing or the Illumina Hiseq or Miseq platforms. Three studies sequenced metagenomes, with one study solely analyzing metagenomic data and the other two pairing metagenomes with 16S metabarcoding (Table 1). A wide variety of diversity metrics were used to quantify alpha diversity across studies. The Shannon index was the most commonly reported, followed by richness, with other metrics (Simpson, Faiths PD, Hills effective species number) included in only a few studies. There was not a single diversity metric reported in every study, but since response ratio is a unitless metric, differing metrics were considered together as alpha diversity.



Figure 2: Study locations from the Amazon, Congo and SE Asia. Studies from the same site are represented by a single dot.

Table 1: Summary of included studies

Reference	Region	Pasture	Crop	Duration of agricultural use (years)	Sampling technique	Sequencing target	Sequencing platform
Cuer <i>et al.</i> 2018	Amazon basin	-	eucalyptus	39	point plot	16s V4	Illumina MiSeq
de Carvalho <i>et al.</i> 2016	Amazon basin	Yes	maize, soy bean, upland rice	>20	point transect	16s V4	Illumina MiSeq
Khan <i>et al.</i> 2018	Amazon basin	Yes	-	38	point plot	16s V4	Illumina MiSeq
Kroeger <i>et al.</i> 2018	Amazon basin	Yes	-	38	-	metagenome	Illumina HiSeq
Mendes <i>et al.</i> 2015	Amazon basin	Yes	soy bean	5: soy bean, >10: pasture	point plot	metagenome	Illumina HiSeq
Navarrete <i>et al.</i> 2015	Amazon basin	-	-	2-4 (months)	point plot	16s V4 / metagenome	454 GS FLX (V4) & Illumina HiSeq (metagenomes)
Rodrigues <i>et al.</i> 2013	Amazon basin	Yes	-	22	point nested	16s V4	454 GS FLX
Meyer <i>et al.</i> 2018	Congo basin	-	manioc, banana	-	point nested	16s V3-V4	Illumina Miseq
Cai <i>et al.</i> 2018	Southeast Asia	-	rubber, <i>Plykentia volubilis</i>	25: Rubber, 4: <i>P colubilis</i>	plot pooled	16s V4-V5	Illumina MiSeq
Kerfahi <i>et al.</i> 2016	Southeast Asia	-	rubber	-	pooled plot	16s V3-V4	Illumina MiSeq
Lan <i>et al.</i> 2017	Southeast Asia	-	rubber	-	pooled plot	16s V3-V4	Illumina MiSeq
Lee-Cruz <i>et al.</i> 2013	Southeast Asia	-	oil palm	20-30	pooled transect	16s V3	Illumina HiSeq
Schneider <i>et al.</i> 2015	Southeast Asia	-	oil palm, rubber	6-16: rubber plantation, 15-40: Oil Palm	-	16s V3-V5	454 GS-FLX
Tin <i>et al.</i> 2018	Southeast Asia	-	oil palm	10	point transect	16s V4	Illumina MiSeq
Tripathi <i>et al.</i> 2012	Southeast Asia	Yes	oil palm, banana, lemongrass, papaya, sugarcane, and tapioca		pooled plot	16s V1-V3	454 GS-FLX
Tripathi <i>et al.</i> 2016	Southeast Asia	-	oil palm	20-30	pooled transect	16s V3 / metagenome	Illumina HiSeq
Wood <i>et al.</i> 2017	Southeast Asia	-	oil palm	25	pooled plot	16s V4	Illumina MiSeq

Diversity

Alpha diversity results were reported in all but one study. In these studies, the majority, (9) reported increases in alpha diversity with conversion ($p > 0.001$), six reported no change, and one study reported a decrease (Figure 3). In contrast, beta diversity was not reported in a majority of studies. Among the eight studies that reported beta diversity, a wide variety of sampling and statistical approaches were used, and the results were highly variable. Significant decreases in beta diversity following conversion were reported in three studies, while two studies reported significant increases, and the remainder reporting no consistent response.

Composition

Bacterial community composition varied across studies, but members of five phyla (Actinobacteria, Firmicutes, Chloroflexi, Acidobacteria, Proteobacteria) were reported in a majority of studies (Figure 3). We observed consistent responses to land use change in each of these five phyla (all $p < 0.01$). The relative abundances of Actinobacteria, Chloroflexi and Firmicutes increased with conversion, while the relative abundance of the remaining two phyla, Acidobacteria and Proteobacteria, decreased (Figure 3). In addition to having overall significant effects, these responses were also remarkably universal across studies (Figure 3). Only two studies reported any changes in abundance that were opposite to the summary effect; Firmicutes were reported to decrease in Cuer *et al.* (2018), and Schneider *et al.* (2015) reported a decrease in Actinobacteria and increase in Acidobacteria with conversion (Figure 4).

Within the five phyla exhibiting consistent responses, we looked for consistencies at finer taxonomic levels, either by analyzing available OTU tables or by compiling findings reported in the papers. Such data were rare among the studies; only three reported responses of at least some classes or orders, and four provided OTU tables. Within these seven studies, we found no consistent responses at the class or order level within the phyla that exhibited consistent responses. Thus, while we have no evidence for common responses at finer taxonomic levels, it should be noted that this hypothesis was tested using far fewer studies than used for testing phylum level hypotheses.

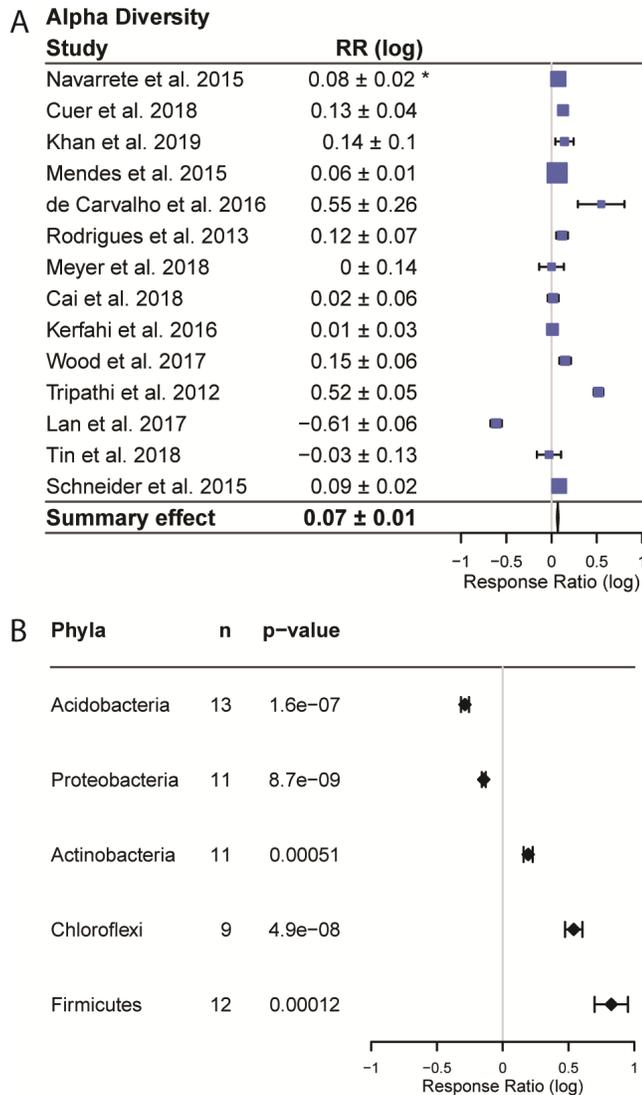


Figure 3: Effects of forest to agriculture conversion on bacterial diversity and composition. (a) Changes in alpha diversity measured as the response ratio (RR). Positive values indicate higher diversity in agricultural areas and negative values indicate higher diversity in forest areas. The bars represent the 95% confidence intervals (CIs) and box size corresponds to study weight in the summary effect size. Summary response ratio was significantly different from zero (two tailed t-tests, $p < 0.001$). (b) Changes in abundance of phyla reported in a majority of studies, including the number of studies reporting each phylum out of 16 studies. * Confidence interval (95%) of the response ratio.

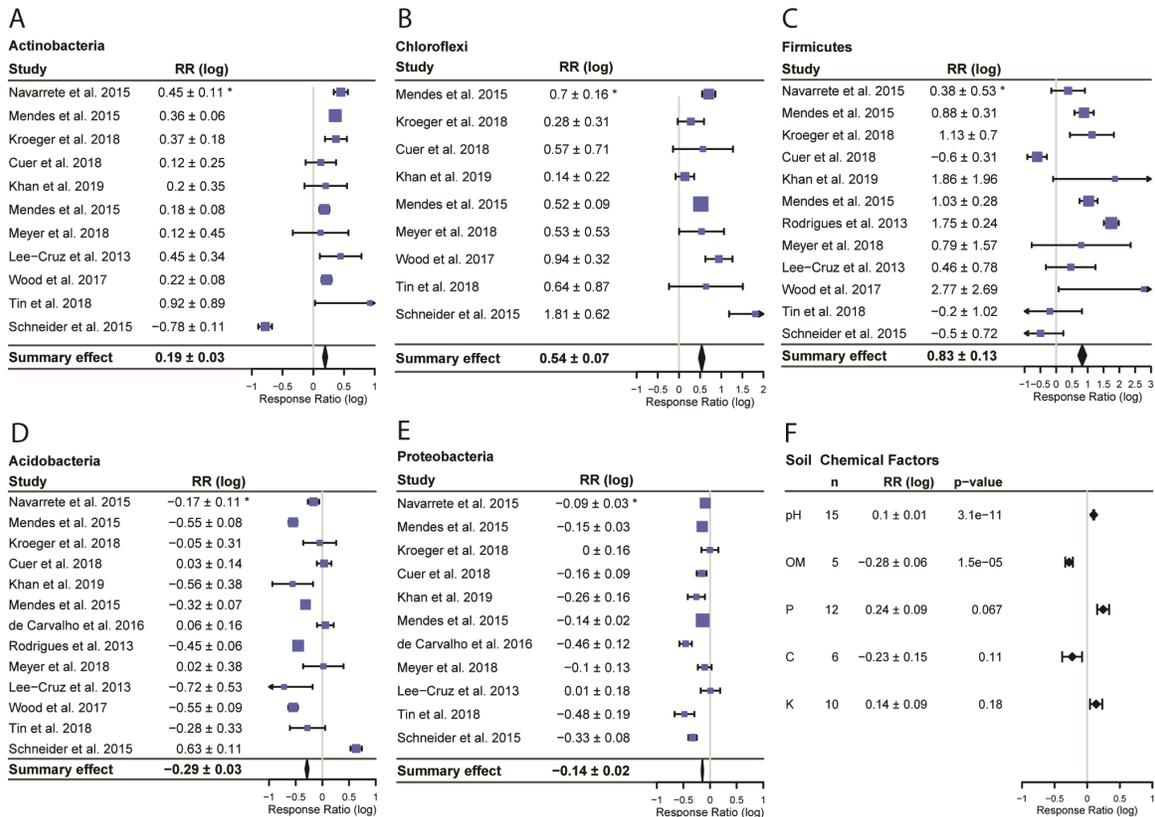


Figure 4: Forest plot for each phylum with a significant summary effect (all $p < 0.001$) (a-e) and summary effects for soil chemical data (f). Bars denote 95% confidence intervals, boxes are centered on means and box size corresponds to study weight for calculating summary effect. * Confidence interval (95%) of the response ratio.

Soil Chemical Factors

The only soil chemical factor that was both reported in a majority of studies and varied significantly with conversion was pH ($p < 0.001$), which increased following conversion (Figure 4). The other two soil chemical factors reported in a majority of studies, potassium (K) and phosphorus (P), did not vary significantly with conversion. Organic matter decreased significantly with conversion, but it was only reported in 5 of the studies.

Discussion

Tropical rainforests harbor greater biodiversity than any other terrestrial ecosystem and are important contributors to global biogeochemical processes (Gardner et al., 2009). These ecosystems are being lost rapidly, primarily from land use conversion for agriculture (Gibbs et al., 2010; Hansen et al., 2013). The effects of land use change

have only recently been studied in bacteria, which comprise a majority of global biodiversity and which mediate most biogeochemical cycles (Hug et al., 2016; Madsen, 2011). By conducting a meta-analysis, we found responses in the composition and diversity of soil bacterial communities to land use change spanning the world's tropical zone.

Diversity

The increase in bacterial alpha diversity following conversion to agriculture differs sharply with commonly reported decreases in the diversity of plants (Ibrahim et al., 2003), animals (Brook, Sodhi, & Ng, 2003; Gardner et al., 2009; Lim, 2017) and fungi (Cai, Zhang, Yang, & Wang, 2018; Kerfahi, Tripathi, Dong, Go, & Adams, 2016; Lan et al., 2017; McGuire et al., 2015; Mueller et al., 2014). This difference may result from ecological differences between bacteria and eukaryotes; for example, bacterial diversity may respond to changes in soil chemical properties, rather than being directly affected by land use change. we found that pH consistently increased with land use change across the studies we surveyed, and others have observed that pH can be correlated with bacterial richness (Fierer & Jackson, 2006; Lauber, Hamady, Knight, & Fierer, 2009). Aboveground productivity could also drive this trend. Agricultural management often promotes high productivity, which could increase soil labile carbon, driving increased bacterial diversity (Dias-Filho, Davidson, & Carvalho, 2001). Alternatively, the apparent increase in bacterial diversity could be an artifact of sampling. Increased alpha diversity at the level of a soil core may not represent landscape-level responses (*i.e.* gamma diversity). Bacteria may actually experience a landscape-level loss of diversity, similar to macro-organisms, if decreases in beta diversity offset or overwhelm increases in alpha diversity (as in Rodrigues *et al.* 2013). If this is the case, the apparent differences may be more methodological than ecological. Unfortunately, we cannot address this hypothesis because beta diversity was not often reported in the studies we surveyed and when measured was assessed with a wide variety of approaches. Consequently, we found that the results of beta diversity assessments were mixed. The difference in responses of eukaryotic and bacterial diversity to land use

change should be investigated further to determine if this results from legitimate ecological differences or differences due to experimental design.

Composition

The commonality of community composition responses at the phylum level is striking and could suggest ecological trait conservation at the phylum level. Land use change is commonly associated with numerous changes to environmental factors (e.g. pH, P, K etc.) and biotic factors (mixing of species, introduction of new species, altered dispersal barriers, etc.). The response of an organism to these changes could depend on traits such as pH tolerance, life history strategies, stress tolerance, or dispersal ability. While the response to land use change is not a direct measurement of a particular trait, it could be thought of as the encapsulation of many individual traits, similar to a polygenetic phenotype. Because traits, especially complex traits, tend to be conserved phylogenetically (A. C. Martiny, Treseder, & Pusch, 2012; J. B. H. Martiny, Jones, Lennon, & Martiny, 2015), responses that are driven by complex combinations of traits should be conserved. I indeed find such conservation here, with consistent declines in Acidobacteria and Proteobacteria, and increases in Actinobacteria, Firmicutes and Chloroflexi. These common responses in composition support the notion of phylum-level conservation of traits that mediate land use change responses.

Functional Consequences

Shifts in the diversity and composition of soil bacterial communities may have important implications for ecosystem function. Higher diversity levels have been associated with increased resistance, resilience, and/or stability of ecosystem function for a variety of aboveground ecosystems (Flynn, Mirotnick, Jain, Palmer, & Naeem, 2011; Hooper et al., 2012; Tilman, Reich, & Isbell, 2012). The generalizability of this trend, however, is an ongoing debate (Cadotte, Carscadden, & Mirotnick, 2011; Srivastava & Vellend, 2005). Community composition has also been reported to affect ecosystem function (Panke-Buisse, Poole, Goodrich, Ley, & Kao-Kniffin, 2014; Swenson, Arendt, & Wilson, 2000; Swenson, Wilson, & Elias, 2000). A recent meta-study found that incorporating microbial composition data with environmental data improves predictions of ecosystem process rates in 53% of cases (Graham et al., 2016), suggesting that

widespread changes to bacterial diversity and composition could impact the functioning of ecosystems. However, we did not explicitly test this hypothesis in our study.

Recommendations for Future Research

The apparent commonality of bacterial responses warrants a more detailed examination, and we suggest several paths forward. First, there is a need to increase the geographic representation of key areas, especially the Congo River Basin. Our comparison is limited by the number of studies fitting our criteria. Tropical ecosystems in general have received considerably less attention from microbial ecologists than temperate areas (Pajares, Bohannan, & Souza, 2016). Encouragingly, bacterial responses to land use change is an emerging area of study, with every study we compared published since 2012. Increasing the number of studies, particularly in the Congo Basin, will allow more rigorous testing of patterns we report, and would provide sufficient power to assess the importance of other characteristics, such as agricultural form and duration of agricultural use, on bacterial responses.

Second, inclusion of other soil organisms such as fungi, nematodes and microarthropods will allow for a more complete understanding of how soil ecosystems are affected by land use change (as in Kerfahi *et al.* 2016). Furthermore, simultaneous sampling of soil biota would allow the direct comparison of responses across large taxonomic groups; this could reveal fundamentally different responses to land use change across these groups. For example, while only five studies of tropical land use change to date have focused on fungi, four reported decreases in alpha diversity with conversion, suggesting that fungi may respond differently to ecosystem conversion than bacteria.

Finally, as more studies are conducted, increased standardization should be adopted for sampling protocols and reporting of findings. The studies assessed here span a breadth of protocols for sampling and a variety of metrics to assess diversity and composition. The generality of findings across this breadth points to the strength of the trends we observed. However, we were hampered in our ability to assess consistent changes in class level abundances and beta diversity due to low levels of reporting and by limited overlap in sampling protocols and analyses. Specifically, we suggest reporting GPS coordinates for every sample, reporting common diversity metrics (Shannon, richness etc.), making

OTU tables and raw sequences available, and we recommend not pooling soil samples (so that spatially explicit analyses are possible). A more standardized set of collection and assessment methods will allow for a more conclusive and thorough analysis of the relationship between land use change and community attributes. If the above steps are taken, we believe it will lead to a much richer understanding of how land use change affects tropical soil communities.

CHAPTER III

CONCLUSIONS

We compared studies spanning a global longitudinal range, with representation from the three largest rainforests, each of which harbors vast biodiversity and high levels of endemism. The studies we compared varied in the primary form of agriculture, duration of agricultural use and research methodology. Despite this variation, we identified consistent shifts in the diversity and composition of bacterial communities in response to the conversion of tropical rainforests to agriculture. Our findings suggest that land use conversion can have predictable effects at a pan-tropical level. With tropical rainforests undergoing dramatic and rapid reductions, it is important to consider the ramifications such changes will have on belowground soil communities and the ecosystem processes they mediate.

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