Consequences of tropical forest conversion to oil palm on soil bacterial community and network structure

Stephen A. Wood [a, b, *], Jack A. Gilbert [c, d], Jonathan W. Leff [e], Noah Fierer [e],
Heather D'Angelo [f], Carling Bateman [g], Seren M. Gedallovich [g], Caitlyn M. Gillikin [g],
Mary R. Gradoville [h], Patahayah Mansor [i], Audrey Massmann [g], Nina Yang [g],
Benjamin L. Turner [j], Francis Q. Brearley [k], Krista L. McGuire [f, g, l]

[a] Yale School of Forestry & Environmental Studies, New Haven, CT 06511, USA
[b] The Nature Conservancy, Arlington, VA 22203, USA
[c] The Microbiome Center, Argonne National Laboratory, Lemont, IL 60439, USA
[d] Department of Surgery, University of Chicago, Chicago, IL 60637, USA
[e] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80302, USA
[f] Department of Ecology, Evolution & Environmental Biology, Columbia University, New York, NY 10027, USA
[g] Department of Biology, Barnard College of Columbia University, New York, NY 10027, USA
[h] College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA
[i] Forest Research Institute Malaysia, 52109 Kepong, Selangor, Malaysia
[j] Smithsonian Tropical Research Institute, Apartado, 0843-03092 Balboa, Ancon, Panama
[k] School of Science and the Environment, Manchester Metropolitan University, Manchester, UK
[l] Institute of Ecology and Evolution, Department of Biology, University of Oregon, Eugene, OR USA

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ABSTRACT

Tropical forest conversion to agriculture is a major global change process. Understanding of the ecological consequences of this conversion are limited by poor knowledge of how soil microorganisms respond. We analyzed the response of soil bacteria to conversion from primary rain forest to oil palm plantation and regenerating logged forest in Malaysia. Bacterial diversity increased by approximately 20% with conversion to oil palm because of higher pH due to liming by plantation managers. Phylogenetic clustering indicated that bacterial communities were determined by environmental filtering. Regenerating logged forests did not have significantly different soil chemistry, which did not correspond with significant differences in bacterial richness, diversity, or the relative abundances of particular taxa. However, there were significant differences in the structure of bacterial community networks between regenerating logged forests and primary forests, highlighting previously unobserved effects of these two land uses. Network analysis highlighted taxa that are potentially central to bacterial networks, but have low relative abundances, suggesting that these rare taxa could play an ecological role and therefore warrant further research.

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1. Introduction

Tropical forests have long been under threat of conversion to other land uses—more than half of the original extent of rain forests has been converted (Asner et al., 2009). Since tropical forests are home to more than two-thirds of all terrestrial plant and animal species (Brooks et al., 2002; Dirzo and Raven, 2003; Gardner et al., 2009), this loss of tropical forest comes hand-in-hand with a loss in biodiversity. Yet this story of conversion and species loss may or may not translate to loss of the huge diversity of soil organisms found under foot.

Soil microorganisms, which make up the bulk of soil diversity, are widely recognized to be essential to the functioning of terrestrial ecosystems. Microbial activity is responsible for many biogeochemical redox reactions (Falkowski et al., 2008). Both negative and positive feedbacks between soil organisms and plant communities contribute to ecological structure and functioning in

the tropics (Bagchi et al., 2010; Kiers et al., 2000; Mangan et al., 2010). Given the importance of soil microorganisms to biogeochemical cycling and plant-soil feedbacks, understanding if soil microbes are threatened by large-scale tropical land-use change is necessary to understand and predict broader functional consequences of land-use change.

An growing body of work has documented how soil microbial communities respond to human-induced environmental change (Thomas W Crowther et al., 2014a,b; da C Jesus et al., 2009; de Carvalho et al., 2016; Fierer et al., 2012; Lee-Cruz et al., 2013; Leff et al., 2015; McGuire et al., 2015; Ramirez et al., 2012, 2010; Rodrigues et al., 2013; Tripathi et al., 2016; Wood et al., 2015). Several consistent patterns have emerged from this work. Changes in the bacterial community are largely governed by changes in soil chemical properties, mainly pH (Lauber et al., 2009; Rousk et al., 2010). Bacterial diversity decreases sharply with decreases in pH, partly due to an associated increase in the relative abundance of taxa such as *Acidobacteria*. By contrast, fungi are less sensitive to changes in pH. Instead, the dominant control on fungi tends to be a combination of factors such as soil carbon, local soil moisture, and plant composition (Barberán et al., 2015; Fierer et al., 2003; Prescott and Grayston, 2013; Prober et al., 2015; Toberman et al., 2008). The response of soil microbial communities to land-use change is in part determined by the properties of the underlying soil, with the greatest difference between forest communities and grassland communities occurring on sandier soils (Thomas W Crowther et al., 2014a,b). This constraint of soil type may be due to lower moisture and carbon holding capacity in sandier soils or inability of sandier soil to buffer against changes in pH, which are dominant controls of fungal and bacterial communities, respectively.

These now robust patterns rely on inference generated from the relative abundance of soil microbes, whether directly or through abundance-weighted diversity metrics. Most microbial taxa are, however, rare (Locey and Lennon, 2016)—i.e. low in relative abundance—and these abundance-weighted metrics may miss possible contributions of rare species. In plant communities, rare species can make important contributions to ecosystem structure and function (Jain et al., 2014; Lyons and Schwartz, 2001). Whether the same is true for microbes remains less well known, but evidence is mounting that loss of rare microbial taxa can play an important role in community structure (Shade et al., 2014) and ecosystem functioning, especially through modifying plant-soil feedbacks (Hol et al., 2015, 2010). Rare taxa, by virtue of being rare, may exhibit different life history strategies than abundant taxa (Murray et al., 2002) and therefore respond differently to land-use change. If this is the case, then understanding their responses may highlight different trends in the response of microbial communities to land-use change. Network analysis, which has been widely used to study the impacts of global change on plant and animal diversity (Ings et al., 2009), may help inform understanding of the ecological role of rare bacteria by highlighting how rare taxa co-occur with well-studied taxa, which could indicate similar ecological roles between rare and well-studied taxa (Ma et al., 2016).

Based on the literature cited above showing that bacterial communities are strongly structured by abiotic conditions, we expected that bacterial community composition and diversity would follow land-use changes that modified soil chemical properties, particularly pH. Because McGuire et al. (2015) found elevated pH under oil palm—but no differences between regenerating and primary forests—we expected that bacterial diversity and community composition would differ between oil palm and the native forest types, but not among the native forest types. For network composition, a chronosequence of abandoned agricultural land showed that fungal networks became more connected in older sites with a shift towards more fungal-dominated food webs (Morriën

et al., 2017). Based on this we developed two competing hypotheses: (H1) bacterial network structure follows patterns observed in fungi and becomes more interconnected moving from disturbed to primary vegetation; (H2) because food webs shift to fungal dominance under primary vegetation, bacterial networks decrease in complexity as fungal communities increase in complexity.

To evaluate our expectations and the consequences of forest conversion on soil microbial composition, we compared bacterial communities from three sites in Malaysia: a primary lowland mixed dipterocarp forest, a regenerating dipterocarp forest that had been selectively logged 50 years ago, and a 25-year old oil palm plantation. Over the past few decades, palm oil, the commercial commodity extracted from the oil palm plant (*Elaeis guineensis;* Arecaceae) has been the most rapidly growing crop in the tropics. Indonesia and Malaysia alone account for more than 80% of all palm oil production and not coincidentally, this region of the world also experiences the highest proportional rate of deforestation (Carlson et al., 2012; Hansen et al., 2013). Thus, oil palm plantations are highly relevant for evaluating the consequences of large-scale tropical deforestation on soil microbial communities.

2. Material and methods

2.1. Site description and field sampling

Soil samples were collected from lowland sites in peninsular Malaysia in the state of Negeri Sembilan, as previously described (McGuire et al., 2015). Briefly, we sampled from three land-use types: primary rain forest (primary forest), forest regenerating from logging 50 years prior (regenerating forest) and an oil palm plantation in active cultivation for 25 years (oil palm). The regenerating and primary forests area are located in the Pasoh Forest Reserve (2°5′ N, 102°18′ W, 80 m asl), with the Dipterocarpaceae family comprising nearly one-third of the basal area of canopy trees (Manokaran et al., 2004). The oil palm plantation was located less than 500 m from the Pasoh Forest Reserve. Climate in this region is aseasonal with mean annual precipitation of 1788 mm and average minimum and maximum temperatures of 22.7 and 33.2 C, respectively. The dominant soil type in the lowland forest plots sampled is Ultisols (Adzmi et al., 2010).

Within each land-use type (primary forest, regenerating forest, and oil palm plantation), three replicate plots (20 × 20 m) were established and five soil samples were collected from each plot during a single sampling event. All sampling plots were at least 1 km away from each other, but selected on the same underlying soil type and slope position. The collected samples were divided into three sampling depths: 0–2 cm, 2–10 cm, and 10–20 cm. All plots were separated by at least 500 m. Sample replicates were composited by depth to one sample per depth, per plot and were placed in sterile plastic bags, sealed and frozen at −20 °C on the day of collection. In the laboratory, all soil samples were passed through a 2 mm sieve, homogenized, and stored frozen at −20 °C until laboratory analyses were performed.

2.2. Laboratory analyses

We amplified and sequenced a portion of the 16 S rRNA gene to assess bacterial communities in a similar manner as described previously (Caporaso et al., 2012). Amplifications were performed on DNA isolates from the MoBio PowerSoil extraction kit (MoBio, Carlsbad, CA), which were the isolates used for prior analysis of soil fungi (McGuire et al., 2015). PCR amplification was performed with the primers 515f and 806r, which included sequencing adapters for the Illumina sequencing platform, and the reverse primer contained a 12-bp barcode unique to each sample. Amplicons