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Land-use type strongly shapes community composition, but not always diversity of soil microbes in tropical China

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ABSTRACT

Forest secondary succession and conversion to an agricultural use are rapidly altering tropical forests, and this alteration has consequences on soil microbial communities. Using high-throughput sequencing of 16S rRNA genes and internal transcribed spacer regions, we compared bacteria and fungi community composition and diversity in soils between the three stages of forest succession (primary forest, PF; secondary forest, SF; pioneer plant community dominated by *Macaranga denticulate* trees, PP) and two agricultural drylands (rubber plantation, RP; *Plukenetia volubilis* plantation, PV) in Xishuangbanna, a tropical region of China, and identified the factors associated with the shift in community composition across the five land-use types. The results indicated that the most abundant bacterial genera (*Bacillus*, *Kitasatospora*, *Nitrospira* and *Streptacidiphilus*) were found at differentially relative abundances among the five land-use types. Through the analysis of indicator species, several bacterial species were significantly associated with the PP site; one to four species were significantly associated to the other sites. Strikingly, almost all fungal genera had site-specific characteristic. Soil properties, especially pH and available P and K, were associated with microbial community composition. Across the three stages of forest succession, bacterial and fungal richness and bacterial alpha diversity had the lowest levels in the earliest stage (PP), but there were no significant differences in microbial richness or diversity between the late stages (PF vs. SF). Compared to PF and SF with their similar bacterial and fungal diversity, the agricultural drylands (RP and PV) had higher bacterial richness but lower fungal richness, indicating that both PF and SF can act as reservoirs for the recolonisation of forest-associated microbes. Overall, these results showed a distinct difference in soil microbe taxonomic composition, especially in fungi, among the various land-use types, even at a very small geographical scale (< 4 km), but no great difference of microbial diversity was found between the late stages of forest succession and agricultural drylands. Tropical forest succession and forest conversion to agricultural drylands strongly affect the distribution of microbial species, whereas microbial diversity may not always tightly follow the same successional trajectories.

1. Introduction

The conversion of primary forest lands to secondary forests and agricultural lands is the principal threat to tropical rainforests in Southeast Asia and elsewhere, which collectively act as the largest reservoir of biodiversity of the world (Wilcove et al., 2013). These land-use changes are the primary drivers of both aboveground and underground biodiversity loss in tropical regions (Nepstad et al., 1999), which in turn affects ecosystem functioning because of the non-sustainable use of land resources. To facilitate the recovery of tropical rainforests, it is important to understand the processes that drive secondary succession, moving from the pioneer to climax stage, at deforested sites. To date, the clear majority of research on succession has focused on plant communities, which is somewhat orderly and shows predictable species changes in space and time following the colonisation of a new environment (Guariguata and Ostertag, 2001). Exhibiting distinct spatial patterns, from scales of micrometers to continents (Fierer and Jackson, 2006; O'Brien et al., 2016), soil microorganisms can respond more rapidly to environmental changes compared to plant communities, and in turn, this affects ecosystem processes, such as nutrient cycling and soil development, because of the vast quantity of microbial biomass and its great diversity (van der Heijden et al., 2008; Delgado-Baquerizo et al., 2017). As the most sensitive indicators of land-use changes and perturbations, the soil

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microbial community is influenced by edaphic (soil pH, nutrients) (Fierer and Jackson, 2006; Tripathi et al., 2012), climatic (Xia et al., 2016; Yao et al., 2017) or land-use intensity (Jesus et al., 2009) factors or other small-scale changes in the plant community (Guo et al., 2016); and the importance of different drivers of change on microbial communities vary at different spatial scales and in different ecosystem types. For example, across North and South America, soil microbial biogeography is controlled primarily by edaphic variables (mainly pH) rather than climatic characteristics and geographic distance (Fierer and Jackson, 2006). In contrast, both soil properties and climate conditions greatly account for the differences in the soil bacterial structure in typical forest ecosystems across eastern China (Xia et al., 2016). Moreover, the factors driving the soil microbial community have been described at a more regional or even continental scale, where the influence of long-lasting distal factors such as geology, climate and associated soil types prevail over that of short-duration proximal factors, such as overlying vegetation composition, do not always hold at local scales, and vice versa (Prescott and Grayston, 2013; O'Brien et al., 2016). In contrast to the relatively large number of studies examining the soil microbial community across broad spatial ranges in terrestrial ecosystems, a comprehensive understanding of the distribution of the soil microbial community at a small scale of land-cover change is still lacking. Thus, gaining a deeper insight into alterations in the composition and diversity of a soil microbial community in relation to land-use and land-cover changes would greatly contribute to the improvement of land management or restoration (Banning et al., 2011; Smith et al., 2015).

In the current study, to elucidate the response of the soil microbial community structure and diversity relevant to forest secondary succession and agricultural lands, we compared soil bacterial and fungal communities from five different land-use types, that is, primary forest, secondary forest, pioneer plant community (dominated by *Macaranga denticulata*, a pioneer tree species), rubber plantation and *Plukenetia volubilis* plantation, in Xishuangbanna, a tropical region of China, and this comparison was done using 16S rRNA and internal transcribed spacer (ITS) ribosomal DNA (rDNA) sequencing, respectively. For the agricultural dry lands, besides rubber (the dominant crop grown in the tropical areas of Southeast Asia), *P. volubilis* Linneo, a promising woody oilseed crop species originating from South America, was selected because this species has been grown continuously in tropical China and other Eastern Asian regions recently (Cai, 2011). This concentration of a range of different land uses in close proximity provided us with an opportunity to study the soil microbial community composition and diversity under the same soil type and climatic conditions while also diminishing the potential effect of dispersal limitation, meaning the detected differences of soil microbial community in response to land-use types can most likely be ascribed to the differences in the soil property and overlying plant community only. The following questions are addressed in the current study: (1) How are the microbial community structure and diversity altered among the different forest succession stages and in the conversion of forest lands to agricultural lands and vice versa? (2) What are the specific microbe groups in each land-use type, and what are the dominant factors in shaping the microbial communities in the field? Our results can provide valid information for the understanding of more effective forest and agricultural managements in tropical China and elsewhere.

2. Materials and method

2.1. Site description and sampling

The study site was located in the Xishuangbanna Tropical Botanical Garden (XTBG) (21°56′N, 101°15′E, altitude 560 m), Xishuangbanna, southwest China. The climate at Xishuangbanna is dominated by the southwest monsoon, which has two distinct seasons: a wet season from May to October and a dry season from November to April. The average annual temperature is 22.9 °C, and the mean annual precipitation is 1500 mm, of which approximately 85% occurs in the wet season; the relative humidity is very high over the years. Based on the FAO soil classification system, the soil is classified as Haplic Lixisol.

Soil samples were collected in the three stages of forest succession and for two agricultural land types, as follows: primary seasonal rain forest (PF), secondary forest (SF), pioneer plant community (PP) and rubber (*Hevea brasiliensis*; RP) and *Plukenetia volubilis* (PV) plantations in XTBG. The five land-use types had the same soil type and were close to each other (< 4 km). The PF was dominated by *Pometia tomentosa* and *Terminalia myriocarpa* with *Barringtonia macrostachya*, *Gironniera subaequalis* and *Saprosma ternatum* in the upper canopy and *Cleidion spiciflorum* and *Pittosporopsis kerrii* as the main subcanopy species. The structure of a normal PF type is complex and multi-layered (Cao et al., 2006). The SF sampling area was previously covered by PF, and the abandoning of deforested areas resulted in the natural regeneration of secondary plant communities with 50–70% canopy coverage. The plant community in the SF was mainly composed of *Bauhinia variegata*, *Spatholobus spp.*, *Callicarpa spp.*, *Kydia calycina*, *Mallotus philippinensis* and *Phyllanthus emblica*. *Digitaria sanguinalis* dominates the herbaceous layer. In typical SF areas, shrubs and epiphytes are very rare. The sampled SF in this study was around 40 years old, and plant species diversity and richness were lower than those in the PF (Cao et al., 2006). The PP was dominated by 5-year old *Macaranga denticulata*, a pioneer tree species, differing considerably from the PF and SF both in plant species and structure, which showed a low and uniform single-layered canopy and a dense herbaceous layer. Two local dominant agricultural dry lands converted from forest were selected: a 25-year-old rubber plantation with a 3 × 8 m density and a 4-year-old intensively cultivated *P. volubilis* plantation with a 2 × 2 m density. The rubber and *P. volubilis* plantations were fertilised with NPK fertiliser at a rate of approximately 80 and 150 kg $ha^{-1}y^{-1}$ in August, respectively, and were both weeded regularly. Because a fast-growing evergreen woody oilseed crop requires high levels of fertiliser to achieve good yield production, more fertiliser was applied in the PV relative to the deciduous rubber trees (Yang et al., 2014). The soil used in the study was sampled in the broader inter-row without fertilisation to avoid any effects of direct fertilisation.

For the soil sampling, PVC tubes (5 cm diameter by 25 cm long) previously sterilised were used to collect the 0–10 cm topsoil layer in a total of 15 plots in May (in the wet season) 2016, with three plots per land-use type with the distance of at least 15 m apart along a scale linear transect. In each plot, four sampling points were established, keeping a minimum distance of 2 m between them; the four samples were pooled to obtain one composite sample per plot. The soil samples were stored at 4 °C for soil physicochemical measurements and at −80 °C for DNA extraction after the removal of root residues using 2 mm mesh.

2.2. Measurement of soil physico-chemical properties

Soil water content was measured by weighing fresh soil samples before and after oven drying at 105 °C for 24 h to a constant weight. The air-drying soil samples were filtered through a 0.149 mm sieve for measuring soil nutrient content; this was conducted at the Public Technology Service Center of XTBG according to the methodology described by Bao (2000). Briefly, soil pH was determined in a 2.5:1 water/soil suspension using a pH meter. The available phosphorus in the soil was determined by the extraction with 0.025 mol L^{-1} HCl and 0.03 mol L^{-1} NH_4F using continuous flow analysis on an Auto Analyzer 3 (SEAL Analytical GmbH, Germany). Total carbon and nitrogen were determined using a Vario MAX CN Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). Hydrolysable nitrogen was measured using the alkali-hydrolysed reduction diffusing method. Determination of the total potassium concentration was carried out by the decomposition of samples using $HClO_4$-HF and detected by an inductively