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Drivers of soil microbial community assembly during recovery from selective logging and clear cutting

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Abstract

1. Despite important progress in understanding the impacts of forest clearing and logging on aboveground communities, how these disturbances affect soil microbial β-diversity and the ecological processes driving microbial assemblages are poorly understood. Further, whether and how the microbial shifts affect vegetation composition and diversity during recovery of post-logged forests remain elusive.
2. Using a spatial grid experiment design in a primary tropical forest intermixed with post-logged patches naturally recovered for half century in Hainan Island, China, we characterized and explained the distance-decay relationships of soil microbial similarities in primary, selectively logged and clear cut forests.
3. Selectively logged sites showed a lower spatial turnover rate of bacterial assemblages based on phylogenetic and taxonomic β-diversity, but a higher spatial turnover rate of fungal assemblages based on phylogenetic β-diversity, suggesting a higher level of phylogenetic variability in fungal composition. Clear cut sites showed lower spatial turnover for both bacterial and fungal assemblages based on the two β-diversity, indicating community homogenization. Main drivers of microbial assemblages shifted from soil properties in primary forest to tree composition in selectively logged sites, whereas microbial-tree associations declined in clear cut sites, leading to stochastically organized microbial assemblages.
4. Synthesis and applications. The increased fungal phylogenetic turnover with tree turnover following selective logging promotes unassisted recovery of plant diversity. In contrast, the decoupling of tree and microbial turnover following clear-cutting suggests restoration approaches based on tree planting, and tree species that have strong associations with bulk soil microbial community should be considered. Our findings advance the understanding of spatial patterns, processes, and drivers of soil microbial assemblages in parallel with tree community recovery during regeneration of post-logged tropical forests, and highlight the importance of coupling assemblage patterns between tree and soil fungal communities for conserving tropical forest biodiversity.

Keywords: β-diversity; soil microbiome; community assembly process; tropical forest; forest management; biodiversity conservation; microbial-tree association

Introduction

Tropical rainforests cover only 7% of the Earth's land surface, yet support more than two-thirds of the global biodiversity (Giam, 2017). However, tropical rainforests experienced long-history logging or clearing, both of which can cause long-lasting impacts on plant and animal communities (Edwards, Tobias, 2014; Socolar et al., 2016). In particular, dramatic shifts have been observed in wildlife and plant groups with specific ecological requirements, such as large vertebrates which need tall trees for nest and plant specialists prefer forest-interior microhabitats (Edwards & Laurance, 2013; Edwards, Tobias, 2014). Although microbial communities in soils may represent the largest component of rainforest biodiversity (Rodrigues et al., 2013), the responses of soil microbial diversity to rainforest harvesting remain elusive, especially microbial β-diversity.

Rodrigues et al. (2013) demonstrated a decreased bacterial β-diversity after clearance and conversion of Amazonian forest to pasture. Historical logging can reduce soil bacterial β-diversity at a large geographic scale from cold temperate coniferous forest to rainforest (Tian et al., 2018). Other studies indicated a higher bacterial β-diversity while a lower fungal β-diversity after rainforest clearance for oil palm compared with selective logging (Lee-Cruz et al., 2013; Kerfahi et al., 2014). These contradictory results suggest that responses of soil microbial β-diversity to rainforest logging might strongly depend on logging intensity and microbial groups. Clarifying soil microbial β-diversity under different logging practices is essential for predicting regional microbial species pool and can directly assist conservation planning.

Microbial community β-diversity can be assessed by spatial composition turnover rate (i.e., increase in dissimilarity) with increasing geographic distance, and is generally composed of species turnover and nestedness (Socolar et al., 2016). Specifically, processes of subtractive homogenization or additive heterogenization, as indicated by extinction of rare species or establishment of invasive species can increase spatial turnover rate, while as indicated by decline but not disappearance of native species or dominance of generalists and invaders may decrease spatial turnover rate (Socolar et al., 2016). Although advances in identifying microbial species have enabled assessments of microbial composition in various habitats, the comparison of spatial

turnover rates between bacterial and fungal composition under logging regimes is unclear, and few studies have disentangled the effects of clear cutting from selective logging.

Forest clearing causes strong losses in vegetation biodiversity and soil carbon and nutrients sequestration (Edwards, Tobias, 2014), which may reduce habitat variability while increase environmental homogenization. Selective logging causes more opportunities for understory species and show little effects on overall plant diversity, which can promote niche differentiation and increase environmental heterogeneity (Edwards & Laurance, 2013). These two logging regimes probably show different effects on soil microbial diversity due to their differential impacts on microenvironment (Edwards, Tobias, 2014; Xu et al., 2015). A quantitative, predictive understanding of soil microbial spatial turnover under different logging regimes is required to clarfy their β-diversity patterns.

Community β-diversity associates closely with assembly processes, which could help us understand how the processes that generate and maintain biogeographic patterns in macroorganisms could operate in the microbial world (Chase & Myers, 2011). For instance, niche-based assembly is predicted to cause decay of compositional similarity with distance due to habitat differentiation, with species differing in terms of their ability to adapt to environmental conditions. Dispersal limitation can shape assembly under the base of neutral niche models, in which an organism's abundance is not influenced by its environmental preferences (Martiny et al., 2011). Stochasticity, which arises from the probabilistic nature of core biological processes, such as births, deaths and species interactions, is another recognized assembly process (Chase & Myers, 2011; Stegen et al., 2013). While soil microbial assemblages are suggested to be co-regulated by these processes (Nemergut et al., 2013; Jiao et al., 2020), the dominant ones under different logging regimes remain unknown. Moreover, few studies have linked the microbial assemblage to recovery of tree communities following logging or clearance.

In this study, we investigated and explained the spatial turnover rate for soil fungal and bacterial communities in tropical forest in Hainan, China that have been subjected to unharvest, clear cutting or selective logging half century ago. Considering that both the patterns and driving processes of soil microbial spatial variation depend on scale of measurement (Martiny et al.,

2011), soil microbial spatial turnover were characterized at a similar scale (11-15 km) under the three regimes with a novel spatial grid design (Fig. S1). We hypothesize that 1) Selective logging increases soil microbial dissimilarity from site to site in parallel with increased environmental heterogeneity, whereas clear cutting decreases soil microbial spatial turnover rates with environmental homogenization; 2) deterministic processes play a more important role than stochastic processes as drivers of the soil microbial spatial turnover in selectively logged sites compared with areas subjected to clear cutting.

Materials and methods

Study site

The study was conducted in the montane tropical forest areas in the Jianfengling forest reserve (JFR) in Southwest Hainan Island, China (18°23'–18°50' N and 108°360'–109°05' E). The mean annual precipitation ranges from 1000 to 3600 mm and the mean annual temperature ranges from 19.4°C to 27.3°C, with a typically dry and (from May to October) wet season (from November to April) receiving 15% and 85% of total annual precipitation, respectively.

The JFR contains 472 km^2 tropical rain forest with two-thirds have been either selectively logged or clear-cut 15-51 years ago. Trees with a diameter at breast height (DBH) > 1 cm were clear cut and 30–40% of the mature stems (DBH > 40 cm) with high commercial values were selective logged. At present, the forest represents a primary forest intermixed with numerous patches regenerated naturally after selectively logging or clear cutting. We established 61 quadrats (25 m × 25 m) across the central 160 km^2 intermixed area using a spatial grid experimental design, with 19, 25 and 17 quadrats in the primary, selectively logged and clear cut patches, respectively, and restricted the distance between quadrats to 15 km to unify sampling scale (Fig. S1). Indeed, the two logging regimes were derived from timber harvest rather field experiment, thus it was difficult to keep the plots distribution absolutely random due to unavoidable dependence of accessibility (Fig. S1).

We recorded all woody stems (hereafter called trees) with DBH $\geqslant$1 cm and identified them to species (Table S2). The studied forest is a combination of ectomycorrhizal and arbuscular

mycorrhizal types, and the balance between both guilds showed no significant difference under the three regimes (Chen et al., 2021). Recovery time (15- 51 years) of these post-logged quadrats has no significant effects on soil microbial composition (Chen et al., 2019). We therefore excluded the recovery year in the following analyses.

Litter sampling and analyses

One composite litter sample was collected in each quadrat using 5 plastic nets (1m × 1m) made from 0.1-cm nucleopore filters, with 4 of them fixed at the corners and the other one at the center of the quadrat. Litter samples were dried at 65 °C to reach a stable weight, and milled to pass a 0.5 mm screen. Litter carbon (C) and nitrogen (N) was measured using dry combustion and the regular Kjeldahl method, respectively. The milled litter was digested in an HNO_3 + $HClO_4$ agent, thereafter litter phosphorus (P) and potassium (K) was determined through flame photometry and calcium (Ca) and magnesium (Mg) was measured on an atomic absorption spectrophotometer (iCE 3000, Thermo Scientific, MA, USA). Litter pH was measured in a litter/water (2:32, V/V) suspension using a pH meter (UB-7 pH/ev Meter; Denver Instrument).

Soil sample collection and physicochemical analyses

Five soil cores (0–10 cm) were collected from each quadrat nearby the litter sampling sites, and were then mixed to form one composite sample. All samples were transferred to laboratory with an ice box after sieving through a 2 mm screen. One part of samples was stored at 4 °C for physicochemical analyses and the other part was stored at −80 °C for microbial analyses.

Soil total carbon (TC) and total nitrogen (TN) were measured on a Shimadzu TOC/TN Analyzer ((Model TOC-VCSH, Shimadzu, Kyoto, Japan). Total phosphorus (TP) and total potassium (TK) was determined via ascorbic acid colorimetric method and atomic absorption method, respectively. Available nitrogen (AN) was detected by alkaline hydrolysis distillation method and available phosphorus (AP) was determined in the $NaHCO_3$ extractant using the molybdate-blue colorimetry method. After extraction with ammonium acetate, we measured soil available potassium (AK), exchangeable calcium (exCa) and magnesium (exMg) content using

atomic absorption spectroscopy (iCE 3000, Thermo Scientific, MA, USA). Soil water content (SWC) and bulk density (BD) was calculated through drying an intact fresh soil core at 105 °C for 24 h. We measured soil pH in a soil/water suspension (1:2.5, w/w) using a pH meter.

Soil DNA extraction, sequencing, and processing

Soil DNA was extracted with the PowerSoil® DNA Kit (MoBio, Carlsbad, CA, USA) and quantified on a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific Inc., USA). The barcode attached primers 515F 5'-GTGCCAGCMGCCGCGGTAA-3' and 806R 5'-GGACTACHVGGGTWTCTAAT-3' were used to amplify the V4 region of bacterial 16S rRNA gene (Caporaso et al., 2012), and the primers ITS2 5'-GCTGCGTTCTTCATCGATGC-3' and ITS5 5'-GGAAGTAAAAGTC GTAACAAGG-3' were applied to amplify the ITS1 region of fungal rRNA gene (Bellemain et al., 2010). The 16S rRNA and ITS amplicons were sequenced on an Illumina HiSeq platform (PE250) by the MAGIGEN Company (Guangzhou, China). Quality check of raw sequences were performed on the Quantitative Insights into Microbial Ecology (QIIME) pipeline (version 1.17). High quality sequences were clustered according to 97% similarity cutoff to generate the operational taxonomic units (OTUs) using UPARSE (version 7.1 http://drive5.com/uparse/). Bacterial OTUs were assigned to taxonomy using the Ribosomal Database Project (RDP) classifier (http://rdp.cme.msu.edu/), and fungal OTUs were assigned based on the UNITE 7.1 database.

Statistical analysis

Spatial turnover rates of soil microbial and plant community composition

Spatial turnover rate was indicated by the slope of distance-decay of microbial dissimilarity (1-similarity) (Martiny et al., 2011). The latitudinal and longitudinal coordinates of each sampling site were used to generate a geographic distance matrix (Table S1). Bray-Curtis and UniFrac (weighted or unweighted) methods were applied to calculate the pairwise taxonomic and phylogenetic distance of microbial communities at OTU level. The slope of the distance-decay relationship was determined as the slope of a linear least squares regression between

ln-transformed geographic distance and ln-transformed microbial distance. We chose the ln-transformed data to yield a better linear fit than untransformed data and to try to avoid skewness of data points. Samples were permuted 999 times to generate random datasets, and assessment of statistical significance of the distance-decay relationship was realized by comparing the observed slope to the values from the random datasets (Martiny et al., 2011). The significance of slopes of pairwise comparisons among logging regimes was also examined by permutation.

Taxonomy information of trees was verified using the online resources: The Plant List (http://www.theplantlist.org/) and Angiosperm Phylogeny Website (http://www.mobot.org/MOBOT/research/APweb/), afterwards the tree taxonomic distance matrix was calculated by Bray-Curtis method. A species-level phylogenetic tree was constructed using online software Phylomatic (http://phylodiversity.net/phylomatic/), and the phylogenetic distance matrix of tree community was measured via UniFrac (weighted or unweighted) method based on the phylogeny that was extracted from the phylogenetic tree. Chao et al. (2006) demonstrated that the Bray-Curtis method would exhibit large positive biases when sampling fractions are not equal or when using small subsamples to make inferences about the larger assemblage. In order to check if the biases from Bray-Curtis would affect the spatial turnover patterns of larger community assemblage in this study, we also used Chao's Jaccard and Chao's Sørensen abundance-based distance to examine turnover rates of microbial and tree communities (Chao et al., 2006).

All soil and litter properties were included in a principle component analysis (PCA) and the first two components (PCA1 and PCA2) accounting for > 40% of the total environmental variance were extracted as new environmental variables. The Euclidean distance of these new environmental variables was calculated to yield the environmental distance matrix. The environmental distance were ln-transformed and plotted against ln-transformed geographic distance to obtain the distance-decay slopes. Linear regressions were generated from the relationships of dissimilarity with every unique distance between every pair of data points, but presented as distance in categories in order to be aesthetic and neat. Although the unavoidable nonrandom distribution of logging quadrats might make the linear regressions sensitive to the quadrats much further away, results from the two regimes could be highly comparable. It is

because both logging regimes have similar arbitrary points that are far away from the other points, and thus could generate similar distance pairs.

Determinants of soil microbial dissimilarity

We performed a multiple regression on the distance matrices (MRM) to test relationships between environmental variables and microbial dissimilarity using the Ecodist R package. Environmental redundancy was assessed prior MRM using the Hmisc R package to exclude highly correlated (Spearman's $\rho^2 \geq 0.5$) variables. A stepwise procedure was applied to remove the non-significant variables, and partial regression coefficients of the significant variables was calculated (Fig, S2) (Martiny et al., 2011).

Soil microbial assembly processes

The relative importance of stochastic processes in microbial assemblages, as measured by unexplained variation in microbial dissimilarity, was examined using a null model analysis based on both taxonomic (Bray-Curtis) and phylogenetic (beta-mean-nearest-taxon-distance, βMNTD) matrices (Fig, S2) (Stegen et al., 2013). For taxonomic composition, the local microbial community was probabilistically assembled 999 times while maintaining constant observed OTU richness and individual numbers. The Bray-Curtis dissimilarity was calculated for each assembly to yield a null distribution. Deviation between observed Bray–Curtis and the null distribution values was standardized to generate the metric of RC_{bray}, We divided the number of pairwise comparisons with $|RC_{bray}| < 0.95$ by the total number of all pairwise compositions to get the fraction of stochastic processes in taxonomic composition (Chase et al., 2011; Stegen et al., 2013). For phylogenetic composition, we randomized the βMNTD by shuffling species names and abundances across the phylogeny tips for 999 times, thereby a null distribution of βMNTD was obtained. Difference between the observed βMNTD and mean of null distribution was referred as the beta-nearest taxon index (βNTI). We divided the number of pairwise comparisons with $|\beta NTI| < 2$ by the total number of all pairwise compositions to get the fraction of stochastic processes in phylogenetic composition (Chase et al., 2011; Stegen et al., 2013). All the analyses were

completed with picante R package.

Results

Distance decay of tree assemblages

Selectively logged and clear cut sites had significantly lower aboveground vegetation biomass ($p < 0.05$) than primary forest, whereas clear cut sites had the highest tree density, followed by selectively logged and primary sites (Table S2), showing an increased proportion of small trees with increasing logging intensity. Slope of the distance-decay relationship for tree dissimilarity increased slightly after selective logging while reduced considerably after clear cutting compared to selectively logged or primary sites (Figs 1a, ac and S4). The significance levels and dynamics of spatial turnover rates among the three management regimes measured by Bray-Curtis dissimilarity were comparable with those measured by Chao's Jaccard and Chao's Sørensen dissimilarities (Figs 1 and S4), implying reliability of the community assemblage patterns measured by Bray-Curtis method in this study, despite its positive biases.

Soil and litter properties

Selectively logged sites had a markedly higher soil AK and exCa while lower litter C than clear cut sites. Soil AN decreased gradually with increasing logging intensity (Table S2). A significant distance-decay relationship for soil and litter properties (see the PCA1 in Table S3) was observed in selectively logged sites. Furthermore, the slope for PCA1 in selectively logged sites (r = 0.373) was steeper than that in primary (r = 0.228, $p > 0.05$, Fig. 1b) and clear cut (r = 0.179, $p < 0.05$, Fig. 1b) sites, indicating an increased dissimilarity of soil environments across sites after selective logging.

Distance decay of soil microbial assemblages

Of the 61 soil samples, a total of 513,159, 704,186 and 489,026 qualified bacterial sequences were obtained for the primary, selectively logged and clear cut sites, respectively. The total qualified fungal sequences were 393,847 in primary forest, 1,127,164 in selectively logged sites and

811,256 in clear cut sites. Bacteria belonging to phyla Acidobacteria, Proteobacteria, Verrucomicrobia, Firmicutes, Actinobacteria, and Planctomycetes were dominant, accounting for more than 91% of the total sequences. The predominant phyla for fungal community were Basidiomycota, Mucoromycota, Ascomycota, and Rozellomycota, which composed more than 96 % of fungal sequences (Fig. S3).

Clear cut sites showed no significant microbial distance-decay relationships based on either taxonomic or phylogenetic diversity while electively logged sites showed significant distance-decay relationships for fungal dissimilarity based on phylogenetic diversity (Figs 2 and S4). The distance-decay slopes for taxonomic dissimilarities were markedly steeper in primary forest than in clear-cut sites ($p < 0.05$, Fig. 2a, 2b). The distance-decay slopes for phylogenetic dissimilarities, however, respond differently to selective logging, with a decrease ($p < 0.05$, Fig. 2c, 2e) in bacterial distance-decay slope while an increase ($p < 0.05$, Fig. 2d, 2f) in fungal distance-decay slope.

Relationships between trees, soil properties and microbial dissimilarity

Over all dissimilarity metrics, the MRM model explained a moderate and significant proportion (R^2 = 26.3% - 51.3%, Table 1) of the bacterial dissimilarity in primary forest while a smaller and significant proportion (R^2 = 11.2% - 26.3%) in selectively logged sites. Soil pH, TP, exMg and SWC showed a significant partial regression correlation (b = 0.050-0.322, $P < 0.05$) with bacterial dissimilarity in primary forests, whereas tree β-diversity contributed the largest partial regression coefficient (b = 0.152-0.314, $P < 0.01$) to bacterial dissimilarity in selectively logged sites. The explained proportion for fungal phylogenetic dissimilarity (R^2 = 20.8% - 24.6%, Table 2) was larger than the taxonomic dissimilarity (R^2 = 10.8%) in selectively logged sites, whereas the explained proportion of the two dissimilarities was comparable in primary forest (taxonomic: R^2 = 27.5%, phylogenetic: R^2 = 22.9%, Table 2). Tree β-diversity was the most important predictor (b = 0.202-0.311, $P < 0.05$, Table 2) of fungal dissimilarity in both primary and selectively logged forests, with geographic distance, elevation, soil pH and soil C:N ratio contributing to smaller but significant partial regression coefficients (b = 0.0001-0.202, $P < 0.05$, Table 2). Notably, only a

small proportion of the soil bacterial and fungal dissimilarities in clear cut forest (R^2 = 6.2% - 8.2%, Table 1 and 2) could be explained by measured soil properties and tree β-diversity.

Collectively, substantial percentages of the spatial variation in bacterial (48.7% - 91.8%) and fungal (75.4% - 93.8%) assemblages remained unexplained, particularly in the clear-cut sites with more than 91% of the variation unexplained. As expected, stochastic processes contributed to considerable proportions of the bacterial (20% - 73%, Table 3) and fungal (57% - 87%, Table 4) assemblages either at the taxonomic or phylogenetic level. In most cases the stochastic processes explained greater variation in clear cut sites than in the primary and selectively logged sites.

Discussion

Our study clarified the effects of post-logging on spatial turnover of bulk soil microbiome in tropical forest, and for the first time disentangled the effects of clear cutting from selective logging. Our hypothesis that selective logging increases microbial spatial turnover while clear cutting decreases microbial spatial turnover is partially supported by the increased fungal phylogenetic dissimilarity in selectively logged sites and decreased fungal taxonomic and phylogenetic dissimilarities in clear cut sites. Soil microbial assemblages in selective logged sites were strongly affected by soil properties and tree composition whereas microbial communities were stochastically assembled in clear-cut areas. These results support our hypothesis that deterministic processes play a more important role than stochasticity in driving soil microbial spatial turnover during recovery after selective logging compared to clear cutting.

Clear cutting considerably reduced bacterial phylogenetic dissimilarity, indicating increased bacterial homogenization at genetic level, which is predicted to decrease population diversity for ecosystem services and reduce ecosystem resilience to disturbance (Olden et al., 2003). In contrast to bacteria, the phylogenetic spatial turnover of fungal assemblages increased after selective logging mainly due to the great influence of increased tree phylogenetic turnover (Table 2), which was in agreement with studies demonstrating profound effects of plant genotypes on fungal composition (Yu et al., 2016). Increased forest gaps created by selective logging may permit greater penetration of direct solar radiation, higher precipitation throughfall, and higher air

temperatures, which consequently provide opportunities for competitive dominance of shade-intolerant, fast-growing tree species (Edwards, Tobias, 2014). Such localized environmental effects could enhance the spatial variation of both plant and fungal communities. However, we only found a slight and non-significant increase in tree composition turnover after selective logging (Fig. 1a, 1c), inconsistent with the markedly increase in fungal turnover (Fig. 2b, 2d, 2f). Perhaps the fungal spatial variation was regulated by the combined effects from plants and other factors, such as soil pH, C:N ratio, and elevation in particular (Table 2). Elevation can indirectly affect soil microbial communities through altering temperature, sunlight, soil physiochemical properties and vegetation composition, and was frequently proved to be a dominant factor shaping microbial spatial distribution patterns (He et al., 2019). Another possible explanation is that post-logging-induced plant residues had strong legacy effects on soil fungal community (Cardenas et al., 2015), overwhelming the effects from tree composition.

Unlike fungi, bacteria are proposed less tightly linked to tree community while more closely associated with soil properties (Hannula et al., 2019), which might support the higher bacterial spatial turnover with higher spatial variation in soil environments (Figs 2 and 3). However, selective logging enhanced the tree-bacterial associations, as the main influential factors affecting bacterial assemblages shifted from soil properties in primary forest to the tree composition in selectively-logged sites (Table 1). Although plant-soil feedbacks are more governed by rhizosphere microbiomes than by bulk soil microbiomes, plant community can significantly interact with bulk soil microbes through various indirect pathways, including litter quality (Fanin et al., 2011), interactions between bulk soil and rhizosphere microbiomes (Bakker et al., 2015), and bulk soil microbially driven release or competition for nutrient with plants (Eldridge et al., 2021). In the selective-logging-induced forest gaps, the new colonizing trees may initially shape the microhabitat through establishing mutualism or antagonism linkages with specific bulk soil bacterial groups. Although we expected that such plant-bacterial interplays would cause high spatial variation in soil environments (Fig. 1b) that may promote bacterial species turnover, we did not find strong supports for deterministic bacterial assemblage. Perhaps the bacterial turnover induced by soil processes was strongly constrained by the enhanced tree-bacterial associations

after selectively logging (Table 1).

The decreased microbial spatial turnover in response to clear cutting indicates community homogenization over space. This was closely related to spatial homogenization of tree composition and soil environments (Fig. 1), and a significant correlation between soil C:N ratio and fungal assembly (Table 2) indicates a selective force on soil microorganisms exerted by clear cutting via substantial modification of soil nutrient conditions. Nevertheless, a larger proportion in microbial assembly could be explained by stochasticity than environmental selection (Table 3), which was conflict with the homogenization of microbial assemblage (Martiny et al., 2011; Chase, 2010)**.** The quantified stochasticity in our study was a total of ecological drift, dispersal limitation and homogenization dispersal as suggested by Stegen et al, (2013). Homogenization dispersal, in which the dispersal is high enough to cause low turnover by overwhelming other processes, can lead to community homogenization (Stegen et al., 2013). Thus, the increased microbial homogenization with more stochastic assembly probably imply a stronger homogenization dispersal of soil microorganisms compared with drift and dispersal limitation, which could be resulted from the remove of diffuse boundaries due to homogenization of soil condition and vegetation composition. Interestingly, the deterministic processes explained greater variation in bacterial phylogenetic β-diversity (64%-80%) than taxonomic β-diversity (27%-40%), which was disagreement with the patterns in plant and animal communities (Barber et al., 2019). Phylogenetic β-diversity of macroorganisms along environmental gradients have been mostly examined at large-scale, regional or continental gradients in climate or habitat (González-Caro et al., 2014). For soil microbial community, however, phylogenetic β-diversity could be examined between communities at relatively finer spatial scales as the case of this study, since microorganisms are sensitive to microhabitat shifts. For fungi, the deterministic processes explained similar variances in taxonomic and phylogenetic β-diversity. Our use of ITS1 in fungal phylogenetic construction may contribute to an inconsistent patterns between bacterial and fungal communities since ITS1 may rise problems in assignment of sequences, and further studies targeting ITS2 or 18S rRNA should be considered to confirm this inconsistent patterns.

Overall, the higher fungal phylogenetic turnover in parallel with environmental and tree

composition heterogenization after selectively log suggests community differentiation across space and species conservation from the broader-scale community under fragmented habitat. Such microbial diversity pattern can benefit tree species co-existence and maintain ecosystem functioning (van der Putten, 2017), which can promote forest recovery in selectively logged sites. We suggest selective logging is better than clear cutting for conserving soil fungal and plant diversity. This reinforces previous reports that selectively logged forest retains most features and species of the original soil and plant communities (Edwards, Tobias, 2014).

The logging and clearance areas in our study present as numerous patches intermixed with primary forest patches (Fig. S1), which is similar to the land-sparing logging approaches that couple protection of old-growth forest blocks with logging elsewhere (Edwards, Gilroy, 2014). Our results provide the evidence, for soil microbial communities, that land-sparing logging could spatially constrain any deleterious biodiversity impacts and benefit species from primary forest, as indicated by the similar species richness between logged and primary forest sites (Chen et al., 2021). Nevertheless, we found higher microbial and tree β-diversity under selective logging than clear cutting, indicating a greater risk of species losses caused by weakened microbial-tree associations after clear cutting. Thus enrichment planting of tree species that could improve soil microbial-tree associations in clear cut sites might be important in alleviating potential species losses. However, further field and greenhouse experiments regarding soil microbial-tree interactions will be required to select tree species.

Conclusion

Our study provides the first evidence for differential effects of selective logging and clear cutting on soil microbial assemblages in tropical forest. Selective logging increased fungal phylogenetic spatial turnover, which could further lead to assemblage divergence over space. There is a higher likelihood that fungal assemblages will diverge with tree composition, promoting plant biodiversity during natural successional trajectories. In contrast, clear cutting increased spatial homogenization of microbial communities and decoupled microbial-tree assemblages. Although forest regeneration is mainly driven by environmental changes including soil physiochemical

properties, microclimate and plant community attributes, with changes in bulk soil microorganisms largely lagging behind, bulk soil microbial shifts can mirror alternations in these environments, and exert feedback effects on the environments. For example, increased fungal phylogenetic β-diversity can increase the spatial component of genetic variability with the end result being the amplification of previously differentiated gene pools (Storfer, 1999; Olden et al., 2003), which would have positive feedback effects on plant genetic diversity due to coupling of microbial and tree phylogenetic biodiversity. In contrast, both taxonomic and phylogenetic homogenization of bacterial community would facilitate the species interactions with limited number and breadth, and lead to weaker selection pressures, thereafter reduce resistance and stability of the microbial community and the ecosystem functions they performed (Olden et al., 2003).

Overall, the reduced microbial β-diversity and decoupling of microbial-tree associations following clear-cutting could cause high risk of biodiversity losses and hinder forest recovery, requiring costly and labor-intensive restoration approaches based on tree planting. However, further studies are necessary to examine influence of different logging regimes and consequent plant recovery on temporal dynamics of bulk soil microbial communities and to test the generality of these findings across other tropical forest ecosystems. Microbial functional β-diversity patterns under different logging regimes should be incorporated into future studies to provide a better understanding of the roles played by soil microorganisms during forest restoration.

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Authors' contributions: JC, RLC and HX conceived the ideas and designed methodology; HX and TSL collected the data; JC, RLC and NGS analyzed the data; JC and RLC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1. Results of the multiple regression on matrices analysis illustrating the contribution of environmental variables to soil bacterial dissimilarity. Both the taxonomic (Bray-Curtis) and phylogenetic (UniFrac) β-diversity were used to calculate community dissimilarity.

	Taxonomic			**Weighted phylogenetic**			**Unweighted phylogenetic**		
Bacterial community	Primary	Selective logging	Clear cutting	Primary	Selective logging	Clear cutting	Primary	Selective logging	Clear cutting
	R^2 = 0.263b	R^2 = 0.112b		R^2 = 0.396b	R^2 = 0.118b		R^2 = 0.513b	R^2 = 0.263b	R^2 = 0.082b
Geographic distance									0.021*
Plant taxonomic diversity		0.297**							
Plant weighted phylogenetic diversity					0.314***				
Plant unweighted phylogenetic diversity								0.152***	
Soil pH				0.200*			0.119**	0.052*	
Soil C:N		0.251*							
Soil TP	0.322*			0.194*			0.089*		

Soil exchangeable Mg			0.050*
Soil water content	0.322*	0.218**	0.093**
Litter Ca		0.180**	0.075**

The variation (R^2) of ln-transformed community distance (distance = 1 – similarity) that could be explained and the partial regression coefficients (b) of the final model is reported (all values are significant at $P \leq 0.001$). The significance level for a partial regression coefficient is * $P < 0.05$, **$P \leq 0.01$, and ***$P \leq 0.001$.

Table 2. Results of the multiple regression on matrices analysis illustrating the contribution of environmental variables to soil fungal dissimilarity. Both the taxonomic (Bray-Curtis) and phylogenetic (UniFrac) β-diversity were used to calculate community dissimilarity.

Fungal community	**Taxonomic**			**weighted phylogenetic**			**Unweighted phylogenetic**		
	Primary	Selective logging	Clear cutting	Primary	Selective logging	Clear cutting	Primary	Selective logging	Clear cutting
	R^2 = 0.275b	R^2 = 0.062b	R^2 = 0.108b	R^2 = 0.229b	R^2 = 0.246b		R^2 = 0.229b	R^2 = 0.208b	
Geographic distance							0.202*		
Plant taxonomic diversity	0.293*	0.311*							
Plant weighted phylogenetic diversity					0.221*				
Plant Unweighted phylogenetic diversity							0.202**	0.180*	
Elevation	0.0004*			0.0003**	0.0002**			0.0001*	
Soil pH							0.079*		
Soil C:N			0.156*						

The variation (R^2) of ln-transformed community distance (distance = 1 – similarity) that could be explained and the partial regression coefficients (b) of the final model is reported (all values are significant at $P \leq 0.001$). The significance level for a partial regression coefficient is * $P < 0.05$, and **$P \leq 0.01$.

Table 3. Relative importance of deterministic and stochastic processes in soil bacterial assemblage. The Bray-Curtis and Mean-Nearest-Taxon-Distance metrics were used to represent taxonomic and phylogenetic assemblages, respectively.

Bacterial assembly processes (%)	Taxonomic			Phylogenetic		
	Primary	Selective logging	Clear cutting	Primary	Selective logging	Clear cutting
Deterministic	40	41	27	79	80	64
Stochastic	60	59	73	21	20	36

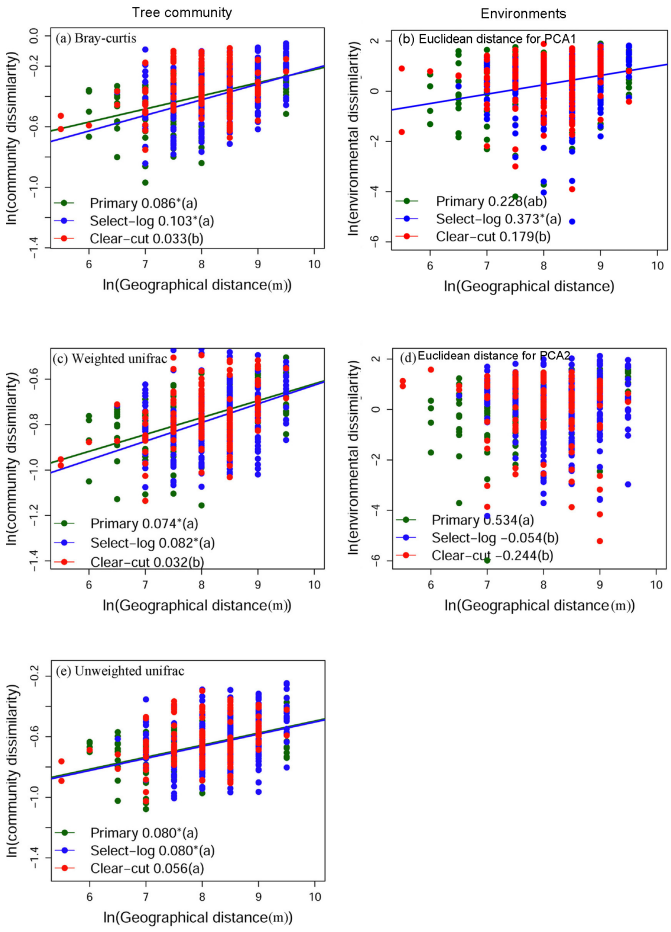
Table 4. Relative importance of deterministic and stochastic processes in soil fungal assemblage. The Bray-Curtis and Mean-Nearest-Taxon-Distance metrics were used to represent taxonomic and phylogenetic assemblages, respectively.

Fungal assembly processes (%)	Taxonomic			Phylogenetic		
	Primary	Selective logging	Clear cutting	Primary	Selective logging	Clear cutting
Deterministic	43	25	13	27	26	32
Stochastic	57	75	87	73	74	68

Figure captions

Figure 1. Distance-decay relationships of the dissimilarity (1-similarity) of tree community and environmental properties (soil and litter properties) in the primary, selectively-logged and clear-cut forests. (a) Taxonomic β diversity of plant community measured by Bray-Curti similarity. (c, e) Phylogenetic β diversity of tree community calculated with weighted and unweighted UniFrac. (b, d) The first two axis (PCA1 and PCA2) of principle component analysis of environmental variables (soil and litter physiochemical properties) were used to represent the new environmental variables. The significant distance-decay relationships were indicated by both regression lines and points, whereas the non-significant relationships were only indicated by the points. The regression coefficients were provided, and the coefficients of significant regressions ($p < 0.05$) were indicated by "*". Different lowercases indicate significant difference of the distance-decay relationships among the three types of forests.

Figure 2. Distance-decay relationships of the dissimilarity (1-similarity) of microbial communities in the primary, selectively-logged and clear-cut forests. (a, b) Taxonomic β diversity measured by Bray-Curtis similarity. (c, d, e, f) Phylogenetic β diversity calculated as weighted and unweighted UniFrac. The significant distance-decay relationships were indicated by both regression lines and points, whereas the non-significant relationships were only indicated by the points. The regression coefficients were provided, and the coefficients of significant regressions ($p < 0.05$) were indicated by "*". Different lowercases indicate significant difference of the distance-decay relationships among the three types of forests.



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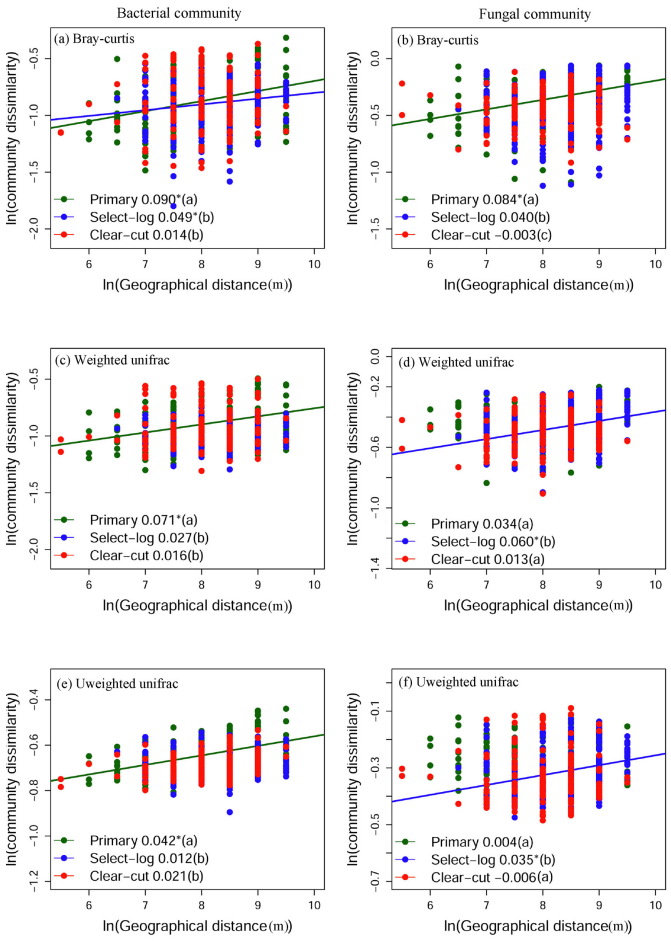

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