

Changes in assembly processes of soil microbial communities during secondary succession in two subtropical forests

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ABSTRACT

Soil microbes re-establish plant diversity and ecosystem functions after disturbance events. Deterministic and stochastic processes are expected to contribute to microbial community assembly during long-term ecosystem recovery. We characterized soil prokaryotic and fungal communities, to determine their assembly patterns, along two chronosequences with early to later successional subtropical forests. Prokaryotic and fungal community composition was more variable in early successional forests but converged in the later successional forests. The community composition was governed by deterministic processes in the early stages, while the relative influence of stochasticity increased in the later stages. Environmental factors that predicted the shift in deterministic and stochastic balance varied within and across successional stages. In particular, the compositional dissimilarity of plant communities strongly predicted the relative influences of the two processes during succession. These findings suggest that the relative influences of deterministic and stochastic processes in shaping microbial community assembly shift during secondary succession. Consequently, plant communities are important predictors of assembly processes in soil microbial communities during long-term ecosystem recovery.

1. Introduction

Understanding ecological processes that control the assembly of soil microbial communities during succession is crucial to predict the response of ecosystems to environmental changes (Nemergut et al., 2013; Zhou and Ning, 2017). Two types of processes, deterministic and stochastic, affect soil microbial assembly. Deterministic processes emphasize the role of biotic and abiotic filtering, which can result in great variation in community composition (higher β diversity) when the environmental conditions are divergent or vice versa (Chesson, 2000; Vellend, 2010). Stochastic processes emphasize the role of probabilistic dispersal and ecological drift that result in patterns of community composition indistinguishable from random assemblages (Hubbell, 2001; Chave, 2004). Both deterministic and stochastic processes influence microbial community assembly (Stegen et al., 2012; Zhou et al., 2014). However, the relative influences of the two processes during long-term ecosystem recovery and the environmental factors involved

are still unclear.

Ecosystem recovery describes biotic and abiotic changes after disturbances. Recent studies have suggested that the strength of selection and stochasticity change through time (Dini-Andreote et al., 2015; Zhou and Ning, 2017). After disturbance events, such as heat or fire, studies on soil bacterial community assembly suggested a predominant influence of deterministic processes in the early stage of recovery because of harsh selection acting on some microbes (Jurburg et al., 2017; Lee et al., 2017). Yet, others suggested reduced deterministic selection because of the increased availability of resources such as carbon after disturbances (Zhou et al., 2014). Although the microbial community assembly following disturbances is further complicated by the types and intensity of disturbance (Jiang and Patel, 2008) and the examined systems (Zhou et al., 2014), disturbances could shift the relative importance of deterministic and stochastic processes (Nemergut et al., 2013). Forest succession after disturbances (e.g., forest harvesting and habitat fragmentation), thus, provides an ideal setting for understanding the

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deterministic and stochastic interplay during long-term ecosystem recovery.

Soil properties, especially soil pH and organic matter, have been documented as the critical factors governing microbial assembly processes during ecosystem development (Dini-Andreote et al., 2015; Tripathi et al., 2018), but plant communities as the driver of microbial community assembly processes have largely been unexplored. Plant communities can affect microbial communities through direct host-microbial interactions and rhizosphere effects (Martínez-García et al., 2015) and indirect mediation of soil physicochemical properties (Zak et al., 2003). Plant diversity (Chen et al., 2017), composition (Prober et al., 2015), and identity (Gao et al., 2015) have been found to influence microbial communities in different ecosystems (Liu et al., 2020). Plant communities' role may be even more pronounced in controlling the community assembly of soil microbes over forest recovery where they serve as the agent to assist ecosystem restoration.

In this study, we examined soil prokaryotic (bacteria and archaea) and fungal community assembly along two chronosequences (decades to hundreds of years after clearcutting) in subtropical forests (Table 1 and Fig. S1). The two chronosequences differ in recovery time but have a similar successional status ranging from early to later successional forests distinguished by dominant plant communities (Peng, 1996; Song et al., 2013). These study sites, therefore, provide an excellent place to evaluate the long-term effects of disturbance and plant communities on soil microbial community assembly. We predict that: (1) if mechanisms underlying microbial community assembly changes during long-term ecosystem recovery, the relative importance of deterministic and stochastic processes should shift with successional stages (Stegen et al., 2012; Zhou et al., 2014); (2) if disturbance (i.e., clearcutting) resets the microbial community assembly, environmental selection should be more important in early successional stages because it is expected that deterministic processes drive the secondary succession toward its climax (Song et al., 2013); (3) if plant communities influence microbial community assembly processes, the shift in the relative importance of deterministic and stochastic processes should be related to changes in plant attributes (e.g., diversity and composition) because plant communities in different successional stages could impose distinct selective pressure on microbial communities.

2. Material and methods

2.1. Study sites

Two long-term subtropical forest chronosequences in the Tiantong

National Forest Park (29°48' N and 121°4'E) and Dinghu Mountain National Natural Reserve (23°06' N and 112°19'E) were used in this study (Fig. S1). They were established in 1983 and 1956, respectively, and both belong to the National Ecosystem Research Network of China (Peng, 1996; Song et al., 2013). Annual mean temperature and total precipitation are 16.2 °C and 1375 mm in Tiantong, and 20.8 °C and 1950 mm in Dinghu. Four forests that were distinguished by the dominant species of plant communities were selected in each region (Table 1 and Figs S1-S2). Stage I in both regions represents the early phase of forest recovery that is dominated by the shrub azalea (*Rhododendron simsii*) or Masson pine (*Pinus massoniana*). Stages II-III represent the transition phase where the shrubs or pine trees are gradually replaced by the typical middle stage tree *Schima superba*. Stage IV is dominated by evergreen broad-leaved trees like *Castanopsis fargesii* and *Cryptocarya chinensis*, which can be treated as the climax phase (Peng, 1996; Song et al., 2013).

2.2. Soil sampling and woody plant survey

Twelve soil cores (0–15 cm depth, 2.5 cm diameter) were taken along the diagonals of 50 m × 50 m plot in each forest in September 2016. All woody plants (diameter at breast height ≥ 1 cm) with a 5 m radius from the sampling points were identified. Soil samples were transported to the laboratory on ice within 12 h after collection and separately stored at –20 °C until DNA extractions or at 4 °C until chemical analysis. To measure pH, total organic carbon (TOC), total phosphorus (TP), and total nitrogen (TN), soil samples were air-dried and sieved through a 100-mesh sieve (0.15 mm). Soil inorganic nitrogen (IN: N-NH₄⁺ and N-NO₃⁻) concentrations were determined after extraction of 10 g fresh soil in 50 ml of 2M KCl using a SmartChem 2000 discrete chemistry analyzer (WESTCO, USA). Soil water content (% SWC) was calculated based on the sample weight before and after drying. Most of these soil properties significantly varied among successional stages (Table S1).

2.3. Molecular analyses for soil microbes

Total DNA was extracted within one week after sampling from 0.5 g soil samples using E.Z.N.ATM Mag-Bind Soil DNA Kit (OMEGA) following the manufacturer's instructions. Barcoded primer sets 515F/907R (Jing et al., 2015) targeting the V4–V5 region of prokaryotic (bacteria and archaea) 16S rRNA genes and ITS3F/ITS4R (Tedersoo et al., 2014) targeting the fungal ITS2 genes were used (Meyer and Kircher, 2010). The 25 µl PCR components contained 2 µl (~10 ng) of template DNA, 5 µl of 5X reaction buffer, 5 µl of High-Fidelity GC buffer, 0.25 µl of

Table 1

The site description and plant community composition across four successional stages in Tiantong and Dinghu subtropical forests.

Forest region	Geographic location	Forest successional stage and estimated forest age (yrs)	Elevation (m)	Slope (°)	Plant community composition (dominant species)
Tiantong	29°48' N, 121°4'E	I (10)	500	25	<i>Quercus fabri</i> + <i>Rhododendron simsii</i>
		II (17)	232	25	<i>Lithocarpus glaber</i> + <i>Loropetalum chinense</i>
		III (90)	145	20	<i>Schima superba</i>
		IV (150)	153	35	<i>Castanopsis fargesii</i>
Dinghu	23°06' N, 112°19'E	I (60)	200	25	<i>Pinus massoniana</i>
		II (70)	300	28	<i>Schima superba</i> + <i>Pinus massoniana</i>
		III (100)	200	25	<i>Castanopsis chinensis</i> + <i>Schima superba</i> + <i>Pinus massoniana</i>
		IV (>400)	100	25	<i>Cryptocarya chinensis</i> + <i>Castanopsis chinensis</i>

High-Fidelity DNA Polymerase (5U/ μ l), 2 μ l (2.5 mM) of dNTPs, 8.75 μ l of ddH₂O, and 1 μ l (10 μ M) of each primer. Amplification was performed at 98 °C for 1 min, with 30 cycles of 98 °C for 10 s, 50 °C for 30 s and 72 °C for 60 s, and a final extension at 72 °C for 5 min for prokaryotes, and at 98 °C for 2 min, with 30 cycles of 98 °C for 15 s, 55 °C for 30 s and 72 °C for 30 s, and a final extension at 72 °C for 30 s for fungi. PCR products were purified using GeneJET Gel Extraction Kit (Thermo Scientific) and sequenced on the Illumina HiSeq PE250 platform at Novogene Co., Ltd, China.

2.4. Bioinformatics analyses

Paired-end sequences were demultiplexed using QIIME v1.8.0 (Caporaso et al., 2010) followed by further processing the raw sequences with DADA2 v1.8 package in R v3.5.3 (Callahan et al., 2016; R Core Team, 2018). The default parameters were used except that we trimmed the forward and reverse reads to 240 bases for 16S rRNA gene and applied no length filtering for ITS region. After quality filtering and merging paired reads, amplicon sequence variants (ASVs) were assigned to taxonomic groups based on the SILVA r138 database (Quast et al., 2013) and the UNITE v8.0 database (Nilsson et al., 2018) for prokaryotes and fungi, respectively, using naïve Bayes classifier (Bokulich et al., 2018). Singletons and 16S rRNA sequences classified as Eukaryota were removed. All ASV tables were rarefied to the smallest sample size to minimize the effect of sequence depths' variation among samples. In total, 2,055,766 (2,055,255 bacteria and 511 archaea) and 2,016,591 (2,010,238 bacteria and 6353 archaea) high-quality sequences for prokaryotes, and 3,452,800 and 3,124,980 sequences for fungi were obtained in Tiantong and Dinghu, respectively. After rarefying to the same number of sequences, 1,541,328 and 1,122,384 sequences for prokaryotes, and 2,259,120 and 2,402,880 sequences for fungi in Tiantong and Dinghu, respectively, were obtained. Sequencing data were deposited in the NCBI under the accession number of PRJNA533708.

2.5. Statistical analyses

All statistical analyses were conducted using R version 3.5.3 and the R package "vegan" v2.4–3 unless stated otherwise (Oksanen et al., 2016; R Core Team, 2018). Community composition (β diversity) was measured as pairwise Bray-Curtis dissimilarity in all analyses. Significant differences in community composition among successional stages were identified using Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) and visualized by Principal Coordinate Analysis (PCoA). The mean pairwise dissimilarities of samples within successional stages were compared by Kruskal-Wallis tests followed by Steel-Dwass means comparisons in R package "PMCMRplus" (Pohlert, 2018).

Two complementary approaches were followed to evaluate the influences of the two assembly processes. First, an abundance-weighted null deviation approach was used (Tucker et al., 2016). This approach maintains the observed metacommunity-level abundance distribution but randomizes the location of individuals to create stochastically assembled communities (Chase and Myers, 2011). The null deviation was measured as the difference of the β diversity (measured as Bray-Curtis dissimilarity) between the observed and randomly assembled communities. A null deviation of zero indicates that the communities follow the stochastic or near-stochastic distribution, whereas a null deviation larger than zero indicates that deterministic processes cause the communities to be more dissimilar than null expectations. We calculated the null deviations for prokaryotic and fungal communities across four successional stages from 1000 stochastic assemblages (Lee

et al., 2017). The permutational analysis of multivariate dispersions (PERMDISP) was used to examine the significance of differences between observed and simulated communities within stages. Differences in null deviations among successional stages were compared by the Kruskal-Wallis test. Second, to explore the influence of stochastic processes on microbial assembly during succession, a neutral community model developed by Sloan et al. (2006) was used. The model fits the predicted frequency of ASVs as a function of their abundance in the metacommunity by one parameter m , which estimates the possibility of a random loss of an individual that will be replaced by dispersal from the metacommunity (Sloan et al., 2006). We assessed the influences of stochastic processes for microbial communities within each stage and across four successional stages (Burns et al., 2016). A generalized R^2 determined the overall fit of the neutral model. The calculation of 95% confidence intervals around all fitting statistics was done by bootstrapping with 1000 replicates.

To explore environmental factors potentially affecting the relative importance of deterministic and stochastic processes, the relationships between microbial null deviations and environmental variables were examined. For plant communities, plant species richness, community composition (Bray-Curtis dissimilarity), evenness, and stand basal area were used. To account for the difference in mycorrhizal status of plants, ectomycorrhizal (EM) plant species were identified (Chen and Chen, 1983; Su et al., 1992). EM richness was highly correlated with plant richness and thus was excluded from further analysis. For soil properties, soil pH, SWC, TOC, TP, TN, and IN were used. We first correlated the mean null deviation of samples with measured environmental variables using the Spearman correlation test. The relationships between null derivations and Euclidean distance matrices of environmental variables within each successional stage were then examined using the Partial Mantel test (controlling influence from spatial distance) to explore how environmental impacts on the assembly processes varied with succession. Expanding the relationships by including between-successional stage comparisons, all pairwise comparisons between null deviations and Euclidean distance matrices of environmental variables were performed using both Mantel and Partial Mantel tests.

3. Results

3.1. Changes in soil microbial community composition

The community composition of soil prokaryotes (PERMANOVA: Tiantong, $F = 9.24$, $P < 0.001$; Dinghu, $F = 11.80$, $P < 0.001$) and fungi (PERMANOVA: Tiantong, $F = 4.07$, $P < 0.001$; Dinghu, $F = 5.26$, $P < 0.001$) was significantly different among successional stages (Fig. 1a and b, e-f). The relative abundance of most phyla varied among successional stages (Fig. S3). For example, compared with other stages, the bacterial phylum *Cyanobacteria* was three times higher at stage II of Tiantong and stages I-II of Dinghu (Tiantong: $\chi^2 = 30.08$, $P < 0.001$; Dinghu: $\chi^2 = 15.31$, $P = 0.002$), and the archaeal phylum *Crenarchaeota* was limited at stage III of Dinghu ($\chi^2 = 13.60$, $P = 0.004$).

The within-stage dissimilarity of microbial communities varied considerably among successional stages (Fig. 1c–d, g–h; Chi-square test: $P < 0.001$ for both prokaryotes and fungi in Tiantong and Dinghu). The dissimilarities in prokaryotic communities at stages I-II of Tiantong and stage I of Dinghu were higher than in later stages, except for the increased dissimilarities at stage IV of Dinghu. For fungal communities, the dissimilarities at stage I of both regions were higher than that at other stages. The distinct differences in community composition imply that mechanisms underlying microbial community assembly could be different among successional stages.

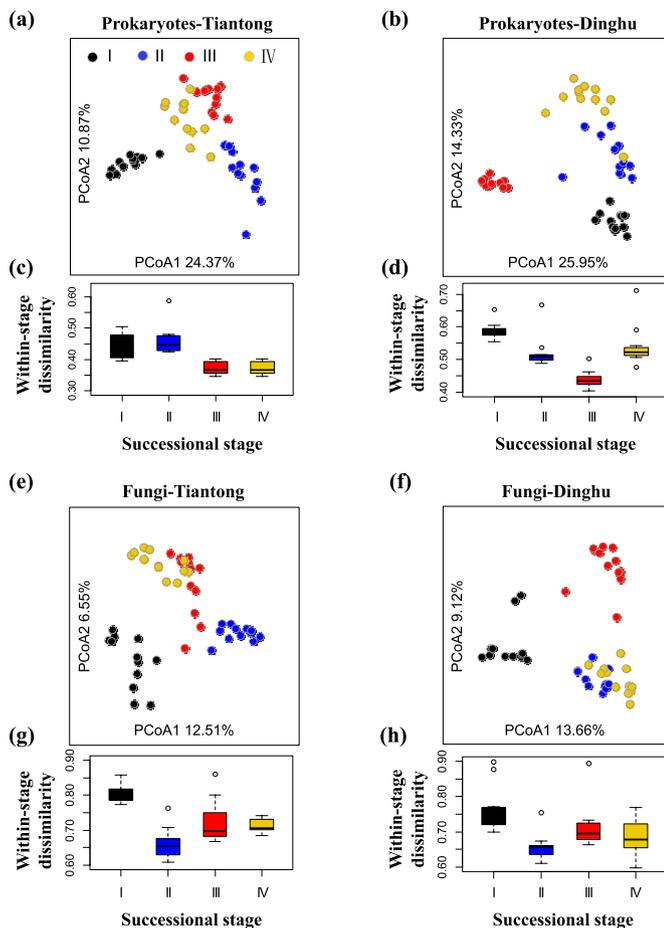


Fig. 1. Principal coordinates analysis (a-b, e-f) and within-stage dissimilarity (c-d, g-h) of prokaryotic and fungal communities among successional stages. Boxplots displaying mean pairwise dissimilarities of samples (Bray-Curtis dissimilarities) within the same successional stage.

3.2. Relative influences of deterministic and stochastic processes

Significant differences in the abundance-weighted null deviations among successional stages were revealed for both prokaryotic and fungal communities (Chi-square test: $P < 0.001$ in both regions), suggesting the balance in deterministic and stochastic processes shifts with succession. All observed communities were significantly different from random assemblages (Table S2; $P < 0.001$ for all comparisons), with larger null deviations in early successional forests than in later stages. The null deviations were high for fungal communities at stage I in both regions and for the prokaryotic communities at stages I-II in Tiantong and stage I in Dinghu, despite the increased null deviations at stage IV in Dinghu (Fig. 2).

The neutral community models showed a higher model fit in communities from stages II-IV than those from stage I in both regions, except for prokaryotes in Tiantong (Figs. S4-S5). The influence of local dispersal was stronger in stages II-IV than in stage I, except for the prokaryotes at stage II in Tiantong and the fungi at stage III in Dinghu. These results agree with null deviation analyses and indicate the increased influence of stochastic processes in the later stages.

3.3. Impacts of environmental variables on microbial community assembly processes

Among successional stages, plant richness was correlated with the mean null deviation of samples (Fig. 3), despite the opposite trend observed in two regions (Spearman correlation; prokaryotes in Tiantong

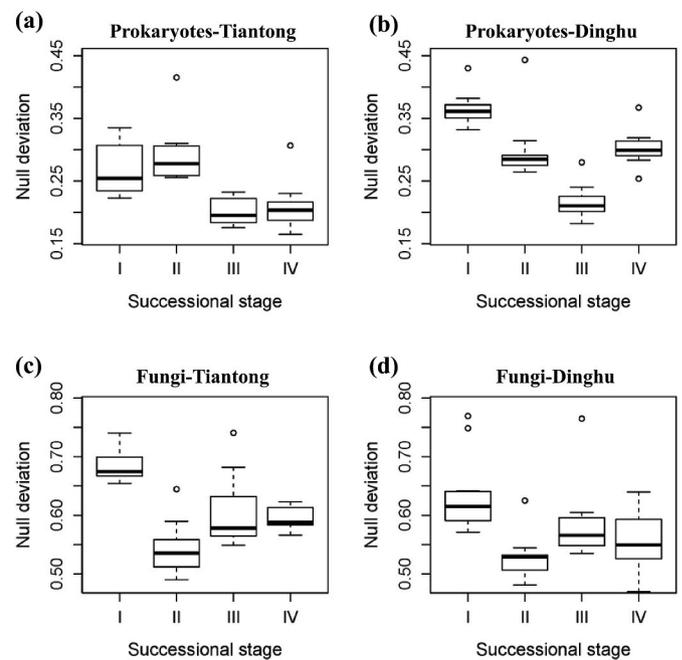


Fig. 2. Boxplots showing the relative changes in deterministic and stochastic processes assessed by null deviation analysis. A null deviation close to zero suggests that stochastic processes are more important in structuring the community, whereas a null deviation larger than zero indicates that deterministic processes are more important.

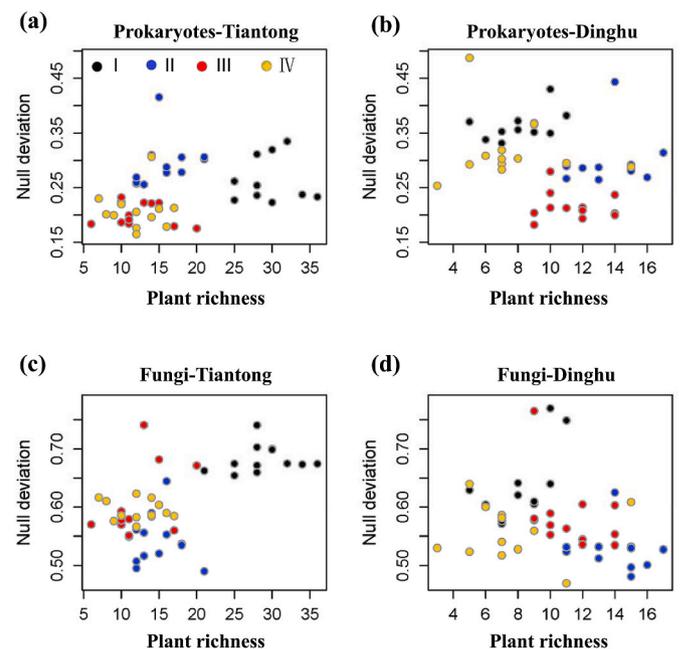


Fig. 3. The relationship between null deviation and plant richness for prokaryotic and fungal communities among successional stages. The mean null deviations within the same successional stage were used.

$r_s = 0.46$, $P = 0.001$, Dinghu $r_s = -0.39$, $P = 0.006$; fungi in Tiantong $r_s = 0.49$, $P < 0.001$, Dinghu $r_s = -0.34$, $P = 0.018$). Within each successional stage, the importance of environmental variables varied (Table S3). For samples from stage I, microbial null deviations were associated with plant compositional dissimilarity, soil pH, and IN in both regions. The microbial null deviations were positively correlated with plant compositional dissimilarity when including between-successional

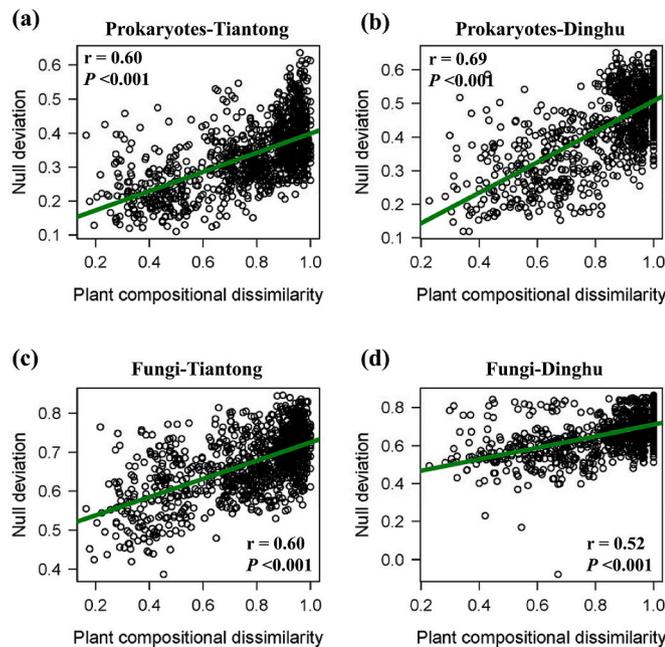


Fig. 4. All pairwise comparisons between null deviation and plant compositional dissimilarity for prokaryotic and fungal communities across successions. The solid lines represent the fitted linear regressions.

stage comparisons (Fig. 4). Observed correlations remained after controlling for spatial distance and were stronger than those between null deviations and recovery time, soil pH, and IN, except for prokaryotes in Tiantong (Table S3).

4. Discussion

4.1. Relative importance of deterministic and stochastic processes shift during secondary forest succession

Our results supported the first prediction that the relative influences of deterministic and stochastic processes governing soil microbial assembly shifted with long-term subtropical forest recovery. We showed marked shifts in soil prokaryotic and fungal community composition and the relative abundance of many dominant phyla during secondary succession in the studied subtropical forests (Fig. 1 and Fig. S3). These findings are in line with previous studies across different ecosystems (Fichtner et al., 2014; Gao et al., 2015; Lee et al., 2017; Bonner et al., 2020). The results of the null deviation analyses and neutral community models (Fig. 2 and Figs. S4-S5) provided further evidence that the importance of selection and stochasticity change through ecosystem recovery, leading to successional trajectories in community structure (Lee et al., 2017; Guo et al., 2018).

We showed further that the relative importance of deterministic processes decreased from the early successional forests, despite deterministic processes generally dominated microbial assembly during the subtropical forest successions. Two chronosequences were investigated that are characterized by similar stages of succession ranging from early to later successional vegetation. Although previous studies hypothesized that the relative influence of deterministic and stochastic processes change through time (Ferrenberg et al., 2013; Dini-Andreote et al., 2015), the consistent trajectory of the deterministic and stochastic balance during successions and strong correlation between microbial assembly processes and plant communities (Figs. 2–4) suggested that strength of selection varied with plant succession/recovery stage despite the different recovery time in two regions.

4.2. Changes in local environment decrease the importance of deterministic selection

Our analyses revealed that deterministic processes were more prominent in early successional forests. Notably, multiple environmental variables were correlated with the null deviation of soil microbial communities, and the correlation coefficients were relatively large in the early stages (Table S3). Despite the potential influences from unmeasured environmental variables (Anderson et al., 2011), the results suggested that heterogeneous environmental selection affected microbial communities assembly in the early successional forests (Ferrenberg et al., 2013). In particular, environmental variables such as plant composition, soil pH, and inorganic nitrogen in the forests might act as strong filters, resulting in variable microbial communities activated from a diverse microbial seed bank that might have been present at the sampled sites already (Lennon and Jones, 2011). As succession proceeds, our results suggested that weak environmental selection contributed to the decreased deterministic processes and increased local dispersal and ecological drift (Table S3). For the prokaryotic communities at the latest stage of Mt. Dinghu, biotic interactions or the development of structured ecological niches might enhance environmental selection after long-term succession but need further evaluation (Fig. S6) (Jackson, 2003; Dini-Andreote et al., 2015).

The importance of deterministic selection after disturbance may be dependent on the examined ecosystems. Stochasticity could be more critical in ecosystems where the environment is relatively homogeneous. In these cases, stochastic processes may prevail and disturbance events decrease the relative influence of stochasticity as shown before (Guo et al., 2018). In contrast, a heterogeneous selective environment strongly dictates what can grow following disturbances with relatively little contribution of stochasticity (Dini-Andreote et al., 2015).

4.3. The impacts of plant and soil properties on microbial community assembly processes

We expected that shift in the deterministic and stochastic balance to be related to changes in plant attributes. Our results in subtropical forests of Mt. Tiantong (Fig. 3a, c) and a recent analysis of grassland microbial community assembly (Ning et al., 2020) supported that the influence of deterministic processes might increase with plant richness. High plant richness could promote environmental heterogeneity through diversification of available resources for soil microbes and feedbacks between plant and microbes (Reynolds et al., 2003; Wardle et al., 2004), and thus enhanced the deterministic selection. The observed negative relationship with plant richness in forests of Mt. Dinghu (Fig. 3b, d) might be explained by variations in identity and mycorrhizal status of dominant plant species. Abundant ectomycorrhizal trees (e.g., *Pinus massoniana* and *Quercus fabri*) could develop strong biotic interactions with ectomycorrhizal fungi (Chen and Chen, 1983; Su et al., 1992), contributing to the more important influence of deterministic assembly in the early successional forests. In addition, *Schima superba* trees dominant in middle successional forests (e.g., stages II-III in Mt. Dinghu as well as stage III in Mt. Tiantong) were likely to suppress microbial interactions due to produced antimicrobial metabolites (e.g., phenolics and saponins) (Daglia, 2012; Zhang et al., 2018).

Our results provided evidence that plant compositional dissimilarity better predicted microbial assembly processes than soil properties during secondary successions (Fig. 4 and Table S3). The influence of soil pH on microbial assembly processes was probably through selective pressure on soil microbial survival and fitness in strongly acidic soil conditions of the studied forests (Tripathi et al., 2018). Similarly, the importance of inorganic nitrogen on microbial assembly processes might be related to the fitness of microbes at different inorganic nitrogen concentrations, such as nitrogen-fixing bacteria in the phylum *Cyanobacteria* and ammonia-oxidizing archaea in the phylum *Crenarchaeota*

(Verhamme et al., 2011; Fuchsman et al., 2019). For the effects of plant communities, the variation in plant composition across successional stages reflect not only the changes in the relative abundance of plant species but also environmental heterogeneity. Increased variation in plant composition may alter the range of litter inputs and root exudates (Reynolds et al., 2003; Wardle et al., 2004), plant-microbe interactions (Martínez-García et al., 2015), and understory microclimates that affect soil microbial fitness (Maestre et al., 2009). The spatiotemporal shifts in plant composition thus reflect changes in the selective environments that operate on soil microbial communities.

To sum up, our work provides further evidence that soil microbial community assembly was governed mainly by deterministic processes but the relative importance decreased with secondary succession, providing critical insights into the responses of ecosystems to environmental change and the prediction of ecosystem recovery after disturbance. The shift in assembly processes may be attributed to changes in aboveground plant communities, highlighting the importance of considering above- and belowground linkages in differentiating soil microbial community assembly processes. We advocate for further studies to assess the robustness of our findings considering the possibility of seasonal, annual, and ecosystem specific variation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2021.108144>.

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