

Effects of forest degradation on microbial communities and soil carbon cycling: A global meta-analysis

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Abstract

Aim: The aim was to explore how conversions of primary or secondary forests to plantations or agricultural systems influence soil microbial communities and soil carbon (C) cycling.

Location: Global.

Time period: 1993–2017.

Major taxa studied: Soil microbes.

Methods: A meta-analysis was conducted to examine effects of forest degradation on soil properties and microbial attributes related to microbial biomass, activity, community composition and diversity based on 408 cases from 119 studies in the world.

Results: Forest degradation decreased the ratios of *K*-strategists to *r*-strategists (i.e., ratios of fungi to bacteria, *Acidobacteria* to *Proteobacteria*, *Actinobacteria* to *Bacteroidetes* and *Acidobacteria* + *Actinobacteria* to *Proteobacteria* + *Bacteroidetes*). The response ratios (RRs) of the *K*-strategist to *r*-strategist ratios to forest degradation decreased and increased with increased RRs of soil pH and soil C to nitrogen ratio (C:N), respectively. Forest degradation increased the bacterial alpha-diversity indexes, of which the RRs increased and decreased as the RRs of soil pH and soil C:N increased, respectively. The overall RRs across all the forest degradation types ranked as microbial C (−40.4%) > soil C (−33.3%) > microbial respiration (−18.9%) > microbial C to soil C ratio (*q*MBC; −15.9%), leading to the RRs of microbial respiration rate per unit microbial C (*q*CO₂) and soil C decomposition rate (respiration rate per unit soil C), on average, increasing by +43.2 and +25.0%, respectively. Variances of the RRs of *q*MBC and *q*CO₂ were significantly explained by the soil C, soil C:N and mean annual precipitation.

Main conclusions: Forest degradation consistently shifted soil microbial community compositions from *K*-strategist dominated to *r*-strategist dominated, altered soil properties and stimulated microbial activity and soil C decomposition. These results are important for modelling the soil C cycling under projected global land-use changes and provide supportive evidence for applying the macroecology theory on ecosystem succession and disturbance in soil microbial ecology.

KEYWORDS

carbon decomposition, forest degradation, land use, microbial community, microbial diversity, microbial metabolic quotient, soil carbon

1 | INTRODUCTION

The frequency and extent of anthropogenic land-use changes are escalating worldwide. Human activity has affected c. 75% of the ice-free area of terrestrial ecosystems, and thus becomes one of the greatest threats to biodiversity conservation and ecosystem services, such as

carbon (C) sequestration (Watson, Luck, Spooner, & Watson, 2014). Conversion of primary or secondary forests to plantations or agricultural systems is a dominant global land-use change (Rudel et al., 2005) and leads to significant soil organic C losses (Guo & Gifford, 2002). For example, conversion of tropical primary forests into cropland, perennial crops and grassland reduced soil C stocks by 25, 30 and 12%,

respectively (Don, Schumacher, & Freibauer, 2011). Microorganisms are the key regulators of soil biogeochemical cycling processes (Prosser et al., 2007; Schimel, 2016). Soil microbial abundance, community composition, activity and ecophysiological adaptation to environmental changes at the community level can shift the C, energy and nutrient flows at the ecosystem level (Schimel, Balser, & Wallenstein, 2007). Therefore, better understanding of how microbial communities respond to land-use changes and feedback to soil biogeochemical cycling beyond the microhabitat scale is crucially needed in both microbial ecology and ecosystem modelling communities (Pointing, Fierer, Smith, Steinberg, & Wiedmann, 2016).

The decomposition of soil organic matter is predominantly influenced by the microbial community composition and activity as well as the soil physicochemical properties (Bailey, Smith, & Bolton, 2002; Fierer, Bradford, & Jackson, 2007; Xu et al., 2016). Forest degradation changes vegetation characteristics (e.g., plant biomass, species composition and canopy structure) and thus exerts substantial impacts on soil properties (e.g., soil C, elemental stoichiometry and pH; Don et al., 2011; Guo & Gifford, 2002). Such changes can significantly affect soil microbial attributes. For example, global pattern studies showed that soil microbial abundance was correlated with soil and climate factors (Pointing et al., 2016; Serna-Chavez, Fierer, & van Bodegom, 2013; Xu, Thornton, & Post, 2013). Fierer and Jackson (2006) reported that soil pH explained the variances of diversity and richness of soil bacterial communities by 70 and 58%, respectively. A high fungi to bacteria ratio is generally associated with high soil C to nitrogen ratio (C:N; Fierer, Strickland, Liptzin, Bradford, & Cleveland, 2009) and low C decomposition rate (Bailey et al., 2002; Malik et al., 2016; Six, Frey, Thiet, & Batten, 2006; Waring, Averill, & Hawkes, 2013). Even within bacterial phyla, the abundance of *Acidobacteria* was negatively correlated with the C mineralization rate, whereas those of *Proteobacteria* and *Bacteroidetes* exhibited a positive correlation (Fierer et al., 2007). Additionally, modelling (e.g., Xu et al., 2014) and meta-analysis (e.g., Xu et al., 2013; Zhou & Wang, 2015) studies reported that the microbial C to soil C ratio ($qMBC$) significantly decreased as the soil C:N increased. Spohn and Chodak (2015) and Spohn (2015) conducted a field study and a meta-analysis, respectively, and found that the microbial respiration rate per unit microbial C (microbial metabolic quotient, qCO_2) increased with increased resource C:N or C to phosphorus ratio. Nevertheless, previous meta-analyses mainly focus on effects of land-use change types, history, climate or soil clay contents on soil C changes (Don et al., 2011; Guo & Gifford, 2002), and the potential influences on soil microbial communities and activity induced by land-use changes are seldom investigated.

In macroecology, the theory of Odum (1969, 1985) on ecosystem succession and disturbance proposes that young and disturbed ecosystems have a lower ratio of *K*-strategists to *r*-strategists than mature and undisturbed ecosystems. To test whether Odum's theory can be applied in soil microbial ecology, we make the following two analogies for the present study. First, primary or secondary forests are presumably more mature and undisturbed ecosystems compared with plantations or agricultural ecosystems during forest degradation. Second, we assume that microbial attributes can be described by the *K*- and *r*-

selected categories (Chen, Chen, Peng et al., 2016; Chen, Chen, Robinson et al., 2006; Fierer et al., 2007; Kaiser, Franklin, Dieckmann, & Richter, 2014; Zechmeister-Boltenstern et al., 2015), similar to those used in plant and animal community ecology. Fungi tend to be *K*-strategists compared with bacteria, because they have larger size, longer turnover time, higher resource use efficiency, lower maintenance respiration to biomass ratio and higher microbial C to soil C ratio (Bailey et al., 2002; Six et al., 2006; Waring et al., 2013). Nevertheless, microbes have highly diverged various structural and functional traits even within the same taxonomic affiliation (Ho, Lonardo, & Bodelier, 2017). In bacterial phyla, for example, *Acidobacteria* and *Actinobacteria* are associated with low-quality resources, especially *Actinobacteria* that have fungi-like filamentous growth form; whereas *Proteobacteria* and *Bacteroidetes* are related to the decomposition in resource-rich environments (Fierer et al., 2007; Strickland, Osburn, Lauber, Fierer, & Bradford, 2009; Zechmeister-Boltenstern et al., 2015). Obviously, it is challenging and debatable to apply such life strategies to microorganisms as to plants and animals, but it has gained more recognition recently and will be of significance in interpreting and predicting the behaviour and responses of microbes to land-use changes and climate change (Ho et al., 2017).

The present study involved a meta-analysis of 408 cases from 119 studies, with the aim of exploring how conversions of primary or secondary forests to plantations or agricultural systems influence soil microbial communities and soil C cycling. We hypothesized that forest degradation indirectly changed soil microbial attributes by altering soil properties (e.g., soil pH and elemental stoichiometry) combined with geographical and climatic factors. We also attempted to apply Odum's (1969, 1985) macroecology theory on ecosystem succession and disturbance in microbial ecology. Specifically, we examined effects of forest degradation on microbial communities at coarse (fungi and bacteria) and fine (four dominant and most reported bacterial taxa, i.e., *Acidobacteria*, *Proteobacteria*, *Actinobacteria* and *Bacteroidetes*) taxonomic resolutions (Ho et al., 2017 and references therein) and tested the hypothesis that forest degradation would decrease the ratios of *K*-strategists to *r*-strategists (i.e., ratios of fungi to bacteria, *Acidobacteria* to *Proteobacteria*, *Actinobacteria* to *Bacteroidetes* and *Acidobacteria* + *Actinobacteria* to *Proteobacteria* + *Bacteroidetes*), and consequently, increase the qCO_2 and soil C decomposition rate.

2 | MATERIAL AND METHODS

2.1 | Data sources

An extensive literature survey was conducted through the ISI Web of Science, Google Scholar and China National Knowledge Infrastructure (CNKI) databases. The keywords and phrases used for the literature search included 'forest' AND 'metabolic quotient' OR ' qCO_2 ' OR 'microbial respiration' OR 'basal respiration' OR 'microbial biomass' OR 'microbial community' OR 'fungi' OR 'bacteria.' To minimize potential uncertainties in the data analysis, the following criteria were applied to select proper studies. (a) The studies selected were all conducted with a paired-plot design using a 'space for time' approach (i.e., for each

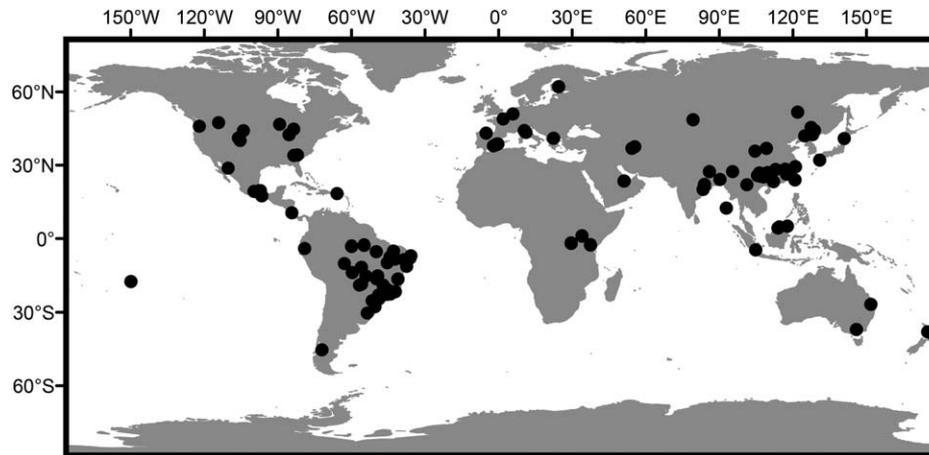


FIGURE 1 A map of the world showing the distribution of the sampling sites in this meta-analysis

paired site, it had been assumed that soil conditions were similar prior and posterior to the forest degradation). The data only from the two ends of the chronosequences were used, following Don et al. (2011). (b) The microbial respiration was measured in laboratory incubation because $q\text{CO}_2$ (Anderson, & Domsch, 1990) and life strategies (Ho et al., 2017) are difficult to be determined in field. (c) The data only from the topsoil layer (i.e., 0–5, 0–10, 0–15 or 0–20 cm depending on the sampling protocols of specific studies) were adopted if the vertical distribution was examined. (d) The data only from the controls were used in instances of manipulation experiments. (e) In the instances where the seasonal dynamics were reported, the data only in the summer or growing seasons (June, July or August for the Northern Hemisphere or December, January or February for the Southern Hemisphere) or wet seasons (for tropical regions) were adopted. A total of 408 cases from 119 papers published from 1993 to February 2017 in the world were included in this synthesis (a list of the data sources can be found in the Appendix; Figure 1).

The dataset included the following variables: (a) three variables of soil properties, namely soil pH, soil organic C and soil total N; (b) three variables related to microbial biomass and activity, namely microbial biomass C, microbial biomass N and microbial respiration (the amount of CO_2 produced in laboratory soil incubation without C or nutrient additions); (c) six variables representing microbial community compositions that were estimated with molecular, physiological, count or phospholipid fatty acid (PLFA) methods, namely fungi, bacteria, relative abundances of *Acidobacteria*, *Proteobacteria*, *Actinobacteria* and *Bacteroidetes* in bacterial phyla; (d) the two most reported bacterial alpha-diversity indexes, namely the Shannon index and operational taxonomic unit (OTU richness); and (e) nine ratios derived from the available data, namely soil C:N ratio, microbial C:N ratio, $q\text{MBC}$, microbial N to soil N ratio ($q\text{MBN}$), $q\text{CO}_2$, fungi to bacteria ratio, *Acidobacteria* to *Proteobacteria* ratio, *Actinobacteria* to *Bacteroidetes* ratio and *Acidobacteria* + *Actinobacteria* to *Proteobacteria* + *Bacteroidetes* ratio. The means (\bar{X}), standard deviations (SD s), and sample sizes (n) of all the variables for each case were extracted from the original papers. If the standard error (SE) was given, then the SD was calculated by:

$$SD = SE\sqrt{n} \quad (1)$$

Otherwise, the SD of 1/10 was assigned (Luo, Hui, & Zhang, 2006). The geographical locations (latitude and longitude) and climate factors [mean annual temperature (MAT) and mean annual precipitation (MAP)] were also obtained from the papers. In the event that MAT and MAP were not provided in the papers, they were extracted from the database at <http://www.worldclim.org/> with the help of the latitude and longitude. All data compiled were numerical data obtained from the tables or text or extracted from the figures with the Origin 7.0 digital plugin (Digitize) (OriginLab Ltd, Norman, OK, U.S.A.).

The land-use types were defined following previous meta-analyses (Don et al., 2011; Guo & Gifford, 2002) as follows. The primary forests were natural vegetations without apparent and reported human impacts, including natural vegetations of forests, shrubs and savannahs (e.g., the South American Cerrado). The secondary forests were naturally developed stands with native species at the deforestation sites. They differed from plantations mainly in terms of human activity involved in the stand establishments. Agricultural systems were divided into grassland, perennial croplands (e.g., sugar cane and coffee) and annual croplands (e.g., maize, wheat and beans). All data were categorized into eight types of forest degradation, as follows: (a) from primary forest to secondary forest, (b) from primary forest to plantation, (c) from primary forest to grassland, (d) from primary forest to perennial cropland, (e) from primary forest to cropland, (f) from secondary forest to plantation, (g) from secondary forest to grassland, and (h) from secondary forest to cropland.

2.2 | Data analysis

We conducted the meta-analysis to evaluate responses of soil properties and microbial attributes to forest degradation with MetaWin 2.1 software (Sinauer Associates Inc., Sunderland, MA, U.S.A.). Specifically, the effect of forest degradation was estimated for each observation as the natural logarithm transformed (\ln) response ratio (RR):

$$RR = \ln(\bar{X}_t/\bar{X}_c) = \ln(\bar{X}_t) - \ln(\bar{X}_c) \quad (2)$$

where \bar{X}_t and \bar{X}_c are the means of the concerned variable in the degraded treatment and original control forest, respectively. If \bar{X}_t and

\bar{X}_c are normally distributed and both are greater than zero, the RR has an approximately normal distribution. Its variance (v) was calculated as:

$$v = \frac{s_t^2}{n_t X_t^2} + \frac{s_c^2}{n_c X_c^2} \quad (3)$$

where n_t and n_c are the sample sizes of the concerned variable in the degraded treatment and original control forest, respectively; and s_t and s_c are the SDs of the concerned variable in the degraded treatment and original control forest, respectively. The weighted response ratio (RR_{++}) was calculated from the RR of individual pairwise comparison between the degraded treatment and original control forest:

$$RR_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k w_{ij} RR_{ij}}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}} \quad (4)$$

where RR_{ij} is the j th comparison ($j = 1, 2, \dots, k$) in the i th group of forest degradation type ($i = 1, 2, \dots, m$). The standard error of RR_{++} [$s(RR_{++})$] was calculated as:

$$s(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}}} \quad (5)$$

where w_{ij} is the weighting factor and estimated as:

$$w_{ij} = \frac{1}{v} \quad (6)$$

To determine whether forest degradation had a significant effect, the 95% confidence interval (95% CI) was calculated as:

$$95\% \text{ CI} = RR_{++} \pm 1.96s(RR_{++}) \quad (7)$$

If the 95% CI overlapped with zero, then the response to forest degradation was considered to be not significant ($\alpha = .05$). The percentage changes in variables caused by forest degradation were measured by:

$$\text{Change (\%)} = [\exp(RR_{++}) - 1] \times 100\% \quad (8)$$

The correlation analysis was used to examine the correlations between different variables. A stepwise regression procedure was used to explore multivariate effects of climate and soil factors on the RRs.

3 | RESULTS

3.1 | Effects of forest degradation on microbial community composition and diversity

Forest degradation consistently decreased the abundance of fungi across all the land-use change types (Figure 2a). Conversions of primary forest to secondary forest, plantation and cropland decreased bacterial abundance, whereas conversions of primary forest to grassland and secondary forest to plantation increased it (Figure 2b). Within bacterial phyla, forest degradation consistently decreased the relative abundances of *Acidobacteria* and *Acidobacteria + Actinobacteria* (Figure 2c,e), but the response directions of *Actinobacteria*, *Proteobacteria*, *Bacteroidetes*

and *Proteobacteria + Bacteroidetes* varied with the land-use change types (Figure 2d,f-h). Forest degradation consistently decreased the fungi to bacteria ratio, *Acidobacteria* to *Proteobacteria* ratio, *Actinobacteria* to *Bacteroidetes* ratio and *Acidobacteria + Actinobacteria* to *Proteobacteria + Bacteroidetes* ratio across all the land-use change types except for the *Actinobacteria* to *Bacteroidetes* ratio for the conversion of primary forest to plantation (Figure 2i-l). Forest degradation significantly ($p < .05$) increased both the Shannon index and richness for all the land-use change types except for the Shannon index for the conversion of primary forest to secondary forest (Figure 2m,n).

3.2 | Effects of forest degradation on microbial biomass and activity

Forest degradation consistently decreased the microbial C and N across all the land-use change types, with decreases in microbial C varying from 25.4% (secondary forest to grassland) to 56.7% (primary forest to cropland) and decreases in microbial N varying from 28.2% (secondary forest to grassland) to 54.5% (primary forest to cropland; Figure 3a,b). However, the response directions of the microbial C:N ratio varied with the land-use change types (Figure 3c). Negative responses of the $qMBC$ and $qMBN$ to all the forest degradation types were found except for a positive response of the $qMBN$ for the conversion of secondary forest to plantation (Figure 3d,e). Forest degradation significantly decreased microbial respiration (Figure 3f), but increased the qCO_2 across all the land-use change types (Figure 3h). Forest degradation increased soil C decomposition rates across all the land-use change types, but the RRs for the conversions from primary forest to grassland, secondary forest to plantation and secondary forest to grassland were not significant (Figure 3g). The overall RRs across all the land-use change types ranked as microbial C (-40.4%) > soil C (-33.3%) > microbial respiration (-18.9%) > $qMBC$ (-15.9%); and those of the qCO_2 and soil C decomposition rate increased, on average, by +43.2 and +25.0%, respectively (Figure 3).

3.3 | Factors affecting microbial responses to forest degradation

Forest degradation significantly decreased soil C and N content (Figure 4b,c), with decreases varying from 8.6 to 61.5% for soil C and from 28.2 to 54.5% for soil N. Inconsistent response directions of soil pH and C:N to forest degradation were found among different land-use change types (Figure 4a,d).

Pooling the data across all the land-use change types, we found that the RRs of the ratios of K -strategists to r -strategists (i.e., fungi to bacteria ratio, *Acidobacteria* to *Proteobacteria* ratio, *Actinobacteria* to *Bacteroidetes* ratio and *Acidobacteria + Actinobacteria* to *Proteobacteria + Bacteroidetes* ratio) consistently decreased and increased with increased RRs of the soil pH and soil C:N, respectively (Figure 5 and Table 1). Both RRs of the Shannon and richness of bacterial diversity increased and decreased with increased RRs of the soil pH and soil C:N, respectively (Figure 5f,i). The RR of the microbial C:N ratio decreased and increased with

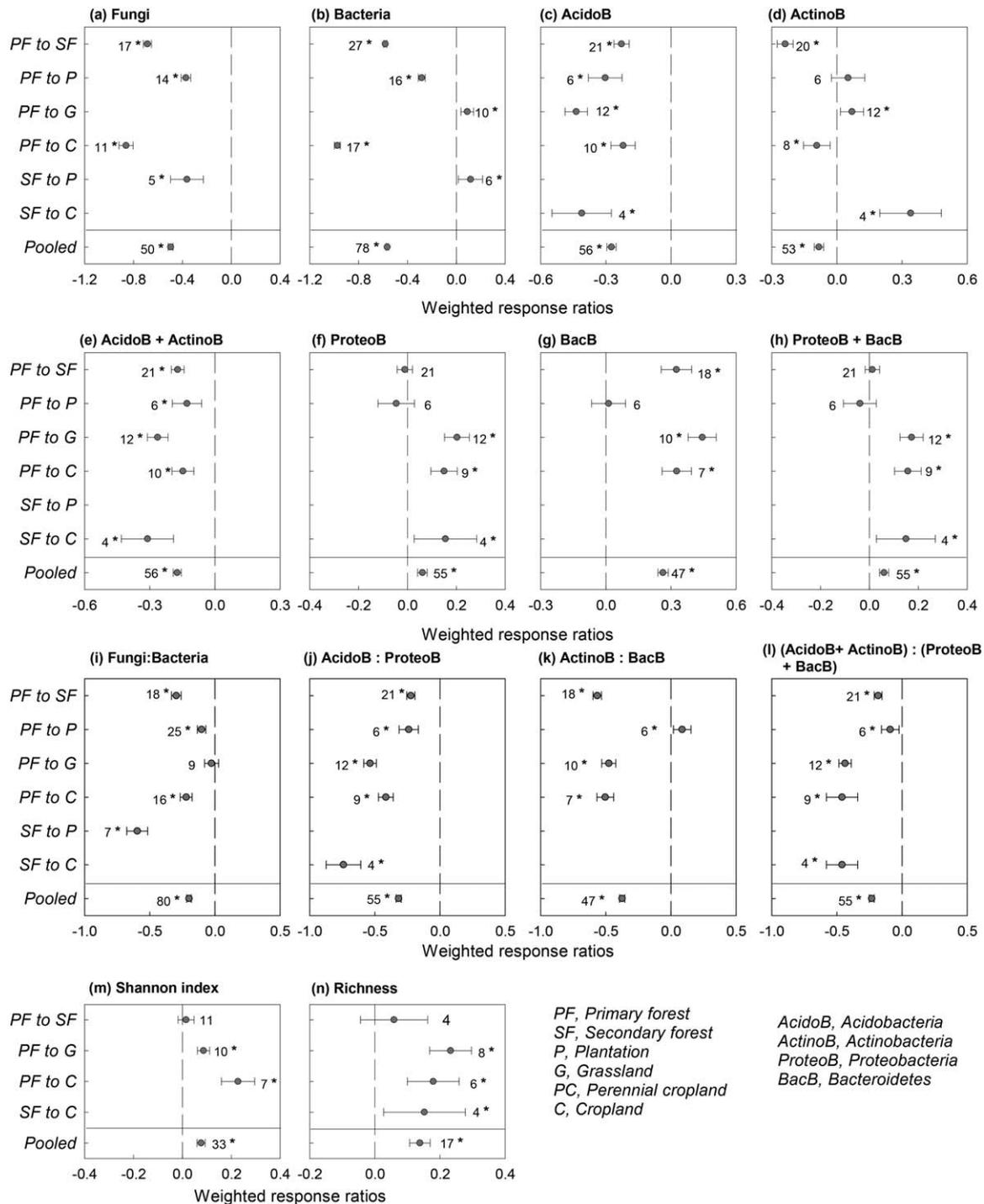


FIGURE 2 Effects of forest degradation on microbial community composition and bacterial diversity by pooled and separate land-use change types. The bars represent the 95% confidence intervals (CIs). The vertical dashed lines are the reference of a response ratio of zero. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant responses

increased RRs of the soil pH and soil C:N, respectively (Figure 5a,g). The RR of the q MBC was negatively correlated with the RR of the soil C:N but positively with the RR of the microbial C:N, whereas the RR of the q CO₂ displayed the opposite correlations (Figure 6).

The stepwise regression analysis showed that the effect of soil properties on the ratios of K -strategists to r -strategists was significant ($p < .05$), but the effect of climate factors was not significant ($p > .05$)

and thus excluded in the regression models (Table 1). However, the MAP contributed significantly ($p < .05$) to the RRs of the q MBC and q CO₂ given that the soil variables were considered (Table 1). The RR of the q MBC tended to decrease as the MAT and MAP increased for most of the land-use change types, whereas the RR of the q CO₂ tended to increase as the MAT and MAP increased (Supporting Information Figure S1).

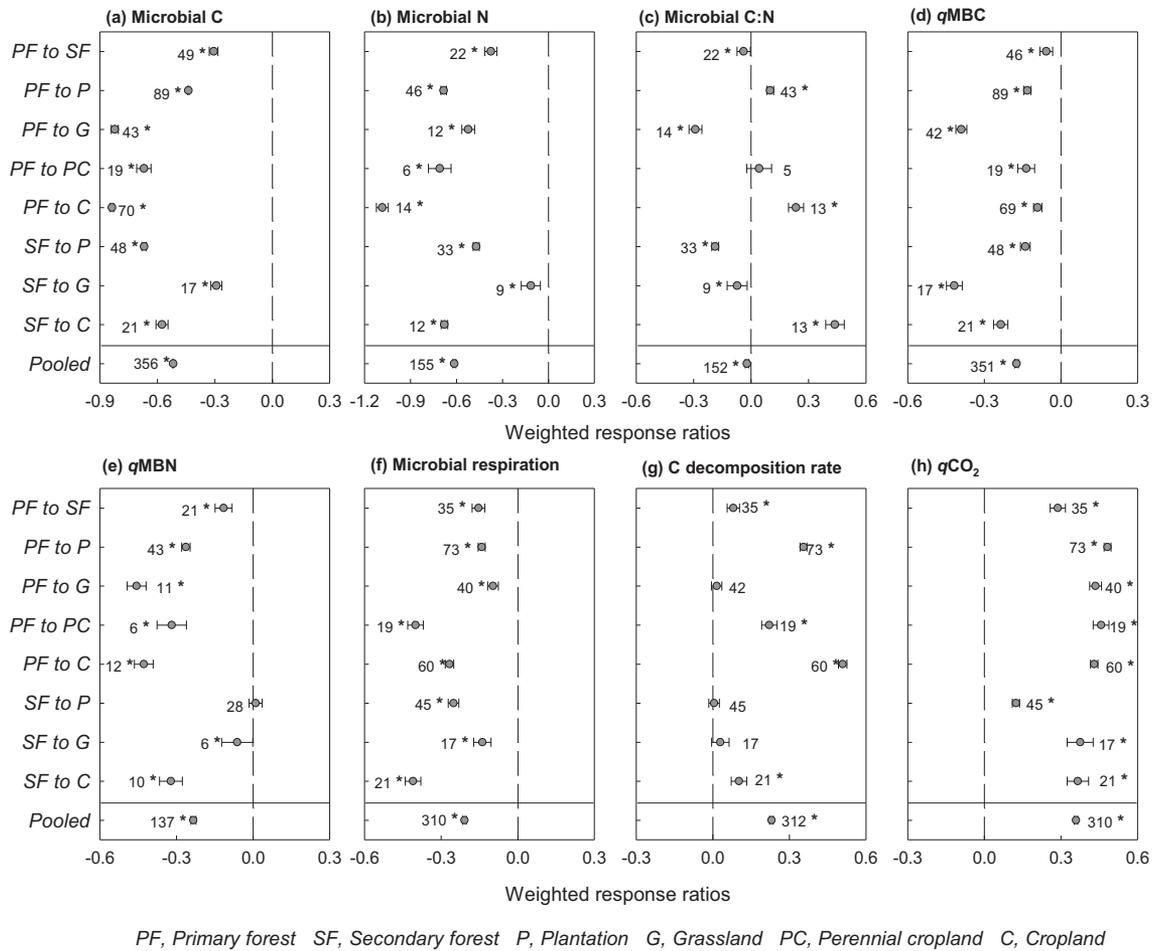


FIGURE 3 Effects of forest degradation on microbial biomass and activity by pooled and separate land-use change types. C decomposition rate = respiration per unit soil C; microbial C = microbial biomass carbon; microbial C:N = microbial biomass carbon to nitrogen ratio; microbial N = microbial biomass nitrogen; qCO₂ = microbial respiration per unit microbial C; qMBC = microbial C to soil C ratio; qMBN = microbial N to soil N ratio. The bars represent the 95% confidence intervals (CIs). The vertical dashed lines are the reference of a response ratio of zero. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant responses

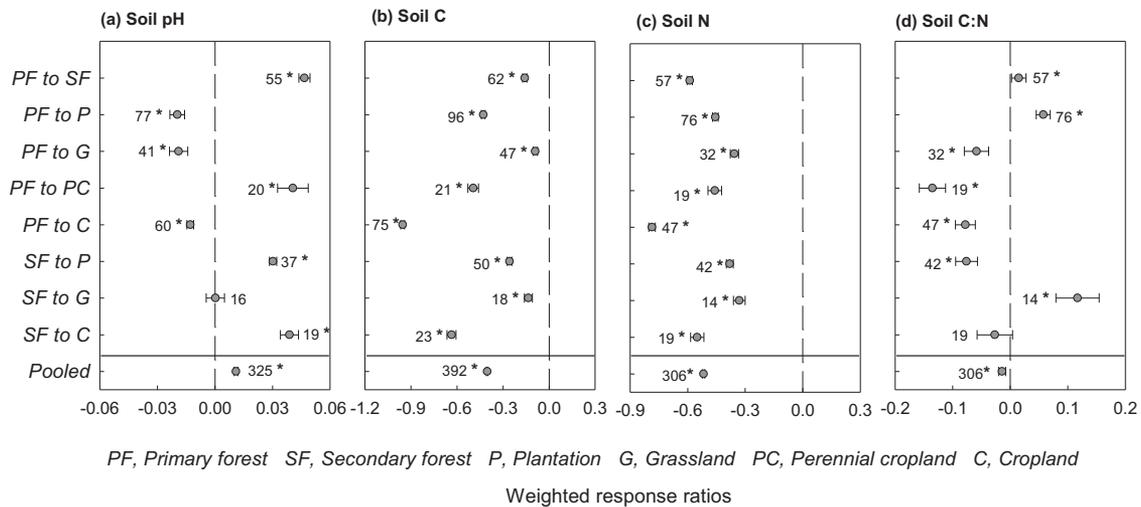


FIGURE 4 Effects of forest degradation on soil properties by pooled and separate land-use change types. Soil C = soil carbon; soil C:N = soil carbon to nitrogen ratio; soil N = soil nitrogen. The bars represent the 95% confidence intervals (CIs). The vertical dashed lines are the reference of a response ratio of zero. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant responses

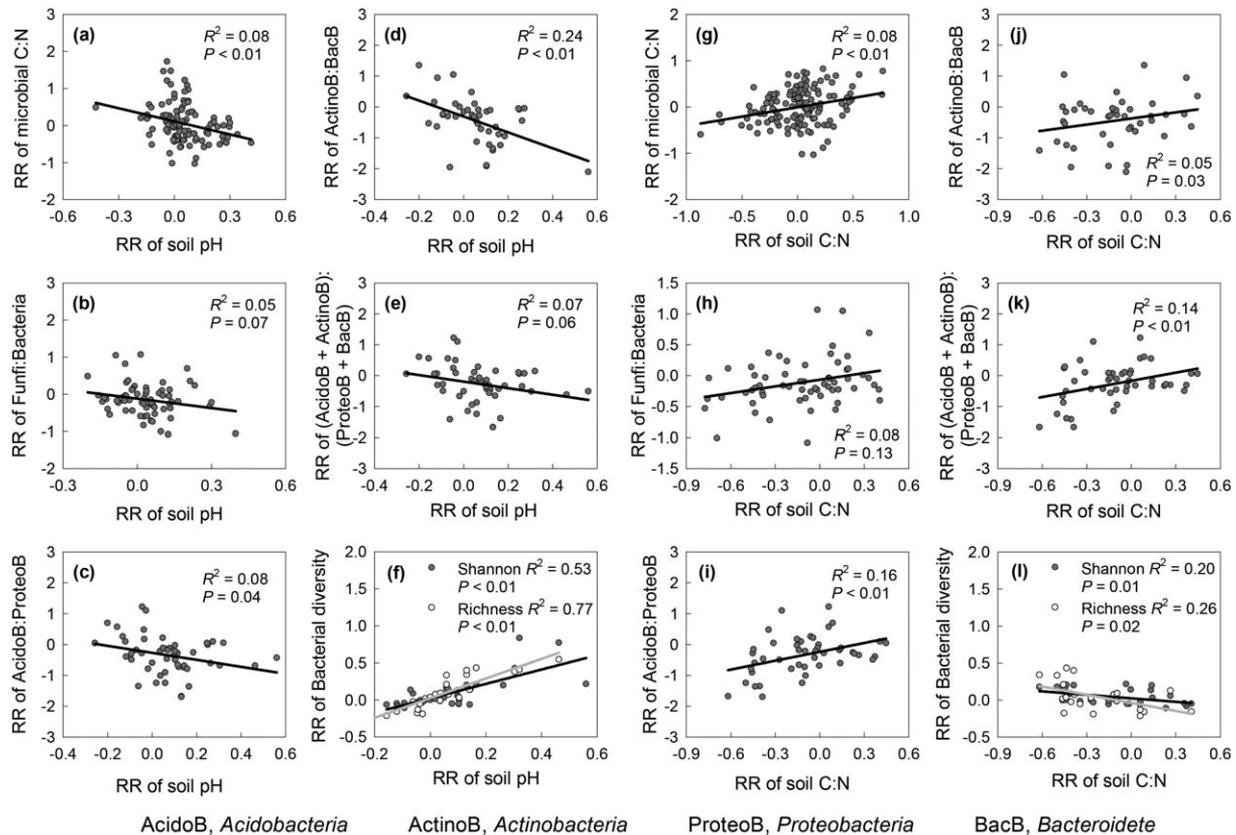


FIGURE 5 Relationships between the response ratios (RRs) of soil properties (soil pH and soil C:N) and the RRs of microbial community composition and bacterial diversity index for pooled land-use change types

4 | DISCUSSION

The present meta-analysis examined responses of soil microbial communities to forest degradation, for the first time, at two taxonomic resolutions based on 408 cases investigated with molecular, physiological, count or PLFA methods from 119 independent studies during the period between 1993 and 2017 in the world. A consistent and general response pattern of soil microbial communities to forest degradation was found; forest degradation significantly

decreased the ratios of *K*-strategists to *r*-strategists, and consequently, increased the microbial metabolic quotient ($q\text{CO}_2$) and soil C decomposition rate by +43.2 and +25.0%, respectively. Overall, our results support the hypothesis that Odum's (1969, 1985) macroecology theory on ecosystem succession and disturbance can be applied in microbial ecology. Below, we discuss possible mechanisms for the observed patterns of microbial attributes in response to forest degradation and their implications in soil C cycling and ecosystem modelling.

TABLE 1 Stepwise regression models of the response ratios (RRs) of microbial variables against soil and climate factors

Dependent variable	Regression model	n	R ²	p value
RR of $q\text{MBC}$	$y = -0.19\text{RR}(\text{C}_{\text{soil}}) - 0.29\text{RR}(\text{C}:\text{N}_{\text{soil}}) - 0.00023\text{MAP} + 0.14$	217	0.28	< .01
RR of $q\text{CO}_2$	$y = -0.39\text{RR}(\text{C}_{\text{soil}}) + 0.40\text{RR}(\text{C}:\text{N}_{\text{soil}}) + 0.00047\text{MAP} - 0.40$	188	0.25	< .01
RR of fungi : bacteria	$y = 0.37\text{RR}(\text{C}:\text{N}_{\text{soil}}) - 0.068$	59	0.09	.02
RR of AcidoB : ProteoB	$y = -0.73\text{RR}(\text{C}_{\text{soil}}) + 1.07\text{RR}(\text{C}:\text{N}_{\text{soil}}) - 0.43$	46	0.50	< .01
RR of ActinoB : BacB	$y = -0.63\text{RR}(\text{C}_{\text{soil}}) - 2.56\text{RR}(\text{pH}) - 0.45$	43	0.36	< .01
RR of RR of (AcidoB + ActinoB) : (ProteoB + BacB)	$y = -0.72\text{RR}(\text{C}_{\text{soil}}) + 0.99\text{RR}(\text{C}:\text{N}_{\text{soil}}) - 0.36$	46	0.47	< .01

Note. The microbial variables include microbial C to soil C ratio ($q\text{MBC}$), microbial respiration per unit microbial C ($q\text{CO}_2$), *Acidobacteria* to *Proteobacteria* ratio (AcidoB : ProteoB), *Actinobacteria* to *Bacteroidetes* ratio (ActinoB : BacB) and *Acidobacteria* + *Actinobacteria* to *Proteobacteria* + *Bacteroidetes* ratio [(AcidoB + ActinoB) : (ProteoB + BacB)]. The independent variables for the stepwise selection procedure include four soil factors [i.e., soil C (C_{soil}), soil N (N_{soil}), soil C:N ratio ($\text{C}:\text{N}_{\text{soil}}$) and soil pH] and two climate factors [mean annual temperature (MAT) and mean annual precipitation (MAP)]. All insignificant terms ($p > .05$) are excluded in the models. The sample sizes (n), determination coefficients (R²) and p values are given.

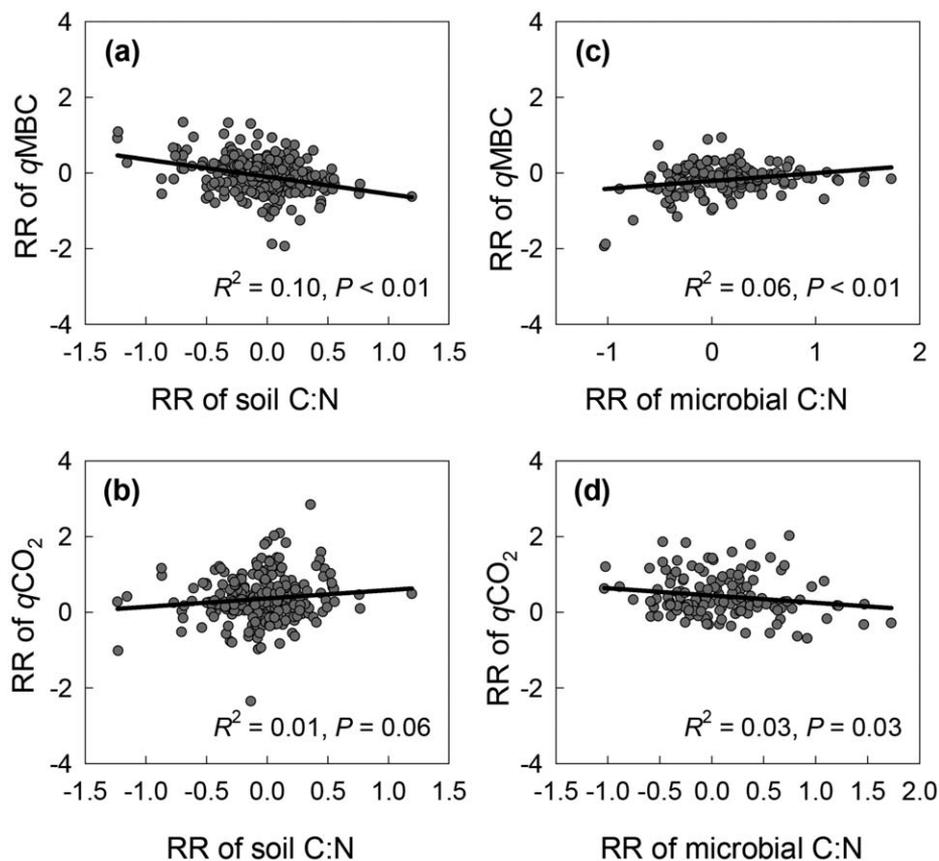


FIGURE 6 Relationships between the response ratios (RRs) of soil or microbial C:N and the RRs of microbial C to soil C ratio (qMBC) or microbial respiration per unit microbial C (qCO_2) for pooled land-use change types

4.1 | Effects of forest degradation on soil microbial communities: Applying the macroecology theory on ecosystem succession and disturbance

Applying the *K*- and *r*-selection framework often used in macroecology to explain microbial responses to forest degradation is challenging and debatable, probably for two main reasons. First, microbes are extremely diversified owing to both abiotic and biotic environmental selection pressures (Ho et al., 2017), and the data of microbial communities with finer taxonomic resolutions are still lacking because of methodological limitations (Ho et al., 2017 and references therein). Second, it is difficult to discern whether the changes in microbial communities are acclimation or adaptation to the new soil conditions caused by forest degradation, because forest conversions to other land-use types usually take years to decades, whereas changes in soil microbial attributes normally occur in days to weeks.

Despite the limitations, we found that forest degradation consistently and significantly decreased the ratio of *K*-strategists to *r*-strategists for almost all the land-use change types (Figure 2), supporting Odum's (1969, 1985) theory on ecosystem succession and disturbance. A recent global synthesis of 85 chronosequences also found that secondary succession had a rising trend in fungi to bacteria ratio (Zhou, Wang, Jiang, & Luo, 2017). Given the fact that it has been effectively applied in recent microbial studies (e.g., Chen, Chen, Peng et al., 2016; Chen, Chen, Robinson et al., 2016; Kaiser et al., 2014; Zechmeister-Boltenstern et al., 2015; Zhou, Wang, Jiang et al., 2017), adopting the

K- and *r*-selection framework for microbial ecology can improve our understanding of the behaviour and responses of microbial communities to land-use changes and global change (Ho et al., 2017) and their functioning in soil systems (Fierer et al., 2007).

Land-use changes modify substrate supplies and soil properties (Don et al., 2011; Guo & Gifford, 2002), hence they affect soil microbial diversity; but the direction and magnitude of the effect are inconclusive. Rodrigues et al. (2013) reported that the conversion of the Amazonian primary rainforests to agricultural systems had a strong negative effect on biodiversity; they suggested that forest degradation increased local diversity of soil bacteria (i.e., increase in alpha diversity), but the communities became more similar across space during the conversion (i.e., decrease in beta diversity). In contrast, de Carvalho et al. (2016) showed that the Amazonian forest degradation increased both alpha and beta diversities of soil bacteria. More studies from tropical regions also reported increased beta diversity during forest degradation (Lee-Cruz, Edwards, Tripathi, & Adams, 2013; Tripathi et al., 2016). In this meta-analysis, we found that forest degradation significantly increased the alpha diversity of bacteria for almost all the land-use change types (Figure 2). The causes for such discrepancies are not clear and, we speculate, might result from indirect effects of forest degradation on microbial indices via changes in the elemental stoichiometry and properties of soils.

Forest degradation significantly altered soil C and N contents and soil C:N stoichiometry (Figure 4), which consequently changed the microbial biomass C:N, *K*-strategists to *r*-strategists ratio and bacterial

diversity (Table 1 and Figures 5 and 6). The relationships between these microbial indices and soil C:N ratio probably result from the stoichiometric constraints, because the *r*-selected copiotrophs generally require more N per unit biomass C accumulation than the *K*-selected oligotrophs (Fierer et al., 2007, 2009; Waring et al., 2013). Meanwhile, the *K*-selected microbes generally have higher biomass C:N ratio than the *r*-selected microbes (Mooshammer, Wanek, Zechmeister-Boltenstern, & Richter, 2014; Zechmeister-Boltenstern et al., 2015). Therefore, stoichiometric constraints are probably one of many factors that influence the microbial communities.

Changes in soil pH during forest degradation also indirectly affected the microbial variables (Table 1 and Figures 5 and 6); they explained 77 and 53% of the variances of the RRs of the richness and Shannon index of bacteria, respectively (Figure 5f). This result is comparable to Fierer and Jackson's (2006) study on 98 soil samples from North and South America, in which soil pH could largely predict the spatial pattern of the bacterial diversity (explaining 70% of the variances of the diversity and 58% of the richness). We also found that the RR of soil pH to forest degradation tended to be correlated negatively with the RRs of the microbial C:N ratio and the *K*-strategists to *r*-strategists ratio (Figure 5); these relationships were partly attributed to the *K*-selected microbes that have a greater capability of tolerating H⁺ concentration than the *r*-selected bacteria (Högberg, Högberg, & Myrland, 2007; Schimel et al., 2007). Nevertheless, the potential mechanisms for the relationships between soil pH and bacterial diversity need more investigation in spite of having attracted wide attention (de Carvalho et al., 2016; Fierer & Jackson, 2006; Kuramae et al., 2012; Stegen et al., 2016). Taken together, the effects of forest degradation on microbial community composition and diversity should be taken into account in forest management practices given the fact that soil microbial communities represent the majority of biodiversity in terrestrial ecosystems and are intimately involved in ecosystem functions (Pointing et al., 2016; Rodrigues et al., 2013).

4.2 | Effects of forest degradation on soil C cycling: Implication in ecosystem modelling

The microbial respiration is the predominant component of soil heterotrophic respiration, which is the largest C flux in soils; and the soil C decomposition rate is determined by biomass and activity of the microbial communities (Xu et al., 2017). We found that forest degradation significantly decreased *q*MBC, but stimulated *q*CO₂ and soil C decomposition rate (Figure 3). These results are in agreement with a recent comprehensive global synthesis by Xu et al. (2017) based on a total of 2,444 observations, in which the *q*CO₂ is about two times higher in cropland than natural ecosystems.

It is increasingly being recognized that microbial community composition plays a crucial role in determining the ecosystem C cycling rates (Fierer et al., 2007; Malik et al., 2016; Schimel, 2016; Strickland, Lauber, Fierer, & Bradford, 2009; Strickland, Osburn et al., 2009; Waring et al., 2013). The increased *q*CO₂ during forest degradation (Figure 3) was associated with the shifts of the microbial community composition from *K*-strategists to *r*-strategists (Figure 2; Fierer et al.,

2007). The *r*-strategist-dominated soils generally have a higher *q*CO₂ than *K*-strategist-dominated soils (Bailey et al., 2002; Blagodatskaya & Anderson, 1998; Fierer et al., 2007; Malik et al., 2016; Six et al., 2006; Tosi et al., 2016; Waring et al., 2013).

Microbial C use efficiency, defined as the ratio of the amount of C used in new biomass (excluding the C excreted in the form of metabolites and enzymes) to the amount of C that has been consumed (Manzoni, Taylor, Richter, Porporato, & Ågren, 2012; Sinsabaugh, Manzoni, Moorhead, & Richter, 2013), is commonly used to quantify how the C is partitioned between growth and respiration. Microbes fed with lower C:N resources often have a higher C use efficiency than microbes fed with higher C:N resources, reflecting an efficient growth and little C release through respiration (Manzoni et al., 2012; Sinsabaugh et al., 2013; Xu et al., 2014). Thus, the negative correlation between the soil C:N and *q*MBC and the positive correlation between the soil C:N and *q*CO₂ are expected (Table 1 and Figure 6), which are also consistent with recent field studies, meta-analyses, modelling research and N addition experiments (Spohn, & Chodak, 2015; Xu et al., 2014, 2017; Zhou & Wang, 2015; Zhou, Wang, & Jin, 2017). Besides, microbes can also mobilize resources by producing specific extracellular enzymes to meet their elemental demand (Mooshammer et al., 2014; Sinsabaugh & Follstad Shah, 2012; Sinsabaugh et al., 2013). Therefore, changes in microbial resource use and synthesis efficiency will reflect the variations in both chemical structure and elemental ratios of the microbial biomass, and eventually, control the soil C and nutrient cycling (Sistla & Schimel, 2012; Sterner & Elser, 2002).

Additionally, our results showed that the RR of the *q*MBC decreased with increased MAT and MAP for most of the forest degradation types, whereas the RR of the *q*CO₂ increased with increased MAT and MAP (Supporting Information Figure S1). Based on previous global analyses, the tropical region has a higher *q*MBC than temperate and boreal regions (Serna-Chavez et al., 2013), whereas the low latitude areas have a significantly lower *q*CO₂ than high latitude areas (Xu et al., 2017). Unfortunately, we do not know why temperature and moisture amplify the effects of forest degradation on the *q*MBC and *q*CO₂ and their interaction with substrate quality and quantity (Davidson & Janssens, 2006; Sihi, Inglett, & Inglett, 2016).

All the discussion above, together with our finding of the close correlations between the RRs of the soil C, microbial C and microbial respiration with forest degradation (Supporting Information Figure S2), suggests that the attributes of soils and microbes during forest degradation interact and feedback on one another (Bailey et al., 2002; Fierer et al., 2007; Xu et al., 2016), and jointly drive the soil C and nutrient cycling. The increased soil C decomposition rate during forest degradation may mainly depend upon the increased microbial activity (i.e., *q*CO₂) given the decreased *q*MBC (Figure 3). Recently, Xu et al. (2017) conducted a global analysis and suggested that the *q*CO₂ can reflect microbial C use efficiency, and consequently, is a direct parameter controlling the soil microbial activity on the C cycling. To simulate the microbial contribution to soil C cycling, however, traditional ecosystem models mostly use the first-order differential equations that typically treat the microbial communities as a single, homogeneous functioning entity (Strickland, Lauber et al., 2009; Xu et al., 2017). The implicit

assumption of these models that microbial communities are functionally equivalent may not be correct. To predict accurately how terrestrial biogeochemical processes respond to land-use changes and global change may require a consideration of changes in microbial community composition and physiological acclimation and/or adaptation to disturbance regimes and environmental changes.

In summary, the present meta-analysis found consistent and predictable patterns of responses of the ratios of *K*-strategists to *r*-strategists, microbial C to soil C ratio and microbial respiration rate to microbial C ratio to forest degradation, supporting the hypothesis that the macroecology theory of Odum (1969, 1985) on ecosystem succession and disturbance can be applied in microbial ecology to some degree. Forest degradation significantly increased the soil C decomposition rate mainly through shifting the microbial community composition and stimulating the microbial activity. Accurate assessment and modelling of soil C budgets under global change scenarios may require a consideration of the microbial community composition and physiological acclimation and/or adaptation to disturbances.

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DATA ACCESSIBILITY

All data supporting this study are extracted from the published papers and provided in the Appendix accompanying this article.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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APPENDIX : DATA SOURCES USED IN THIS STUDY

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