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Ingeniería en Ecosistemas

Effect of passive restoration on soil bacterial communities and factors associated in the major terrestrial biomes

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16 de julio de 2021, ciudad de Tena, Napo, Ecuador

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Abstract

Passive restauration is a common strategy for the recovery of the structure and functionality of forests throughout the world. The degree to which this has occurred is usually evaluated through the study of the plant and animal species present, and soil properties, while little attention has been paid to changes in the communities of soil microorganisms. In order to elucidate the influence of passive restoration in different terrestrial biomes on soil bacteria communities, microbial biomass, and the physical and chemical properties of soil, the present study undertook a meta-analysis of 82 articles to answer the following questions: (i) Does the resilience of soil microbiota and the physical and chemical properties of the soil after of a passive restoration process vary among terrestrial biomes? (ii) What are the levels of soil microbiota and the physical-chemical properties of restored forest compared with primary forest, within the different biomes? (iii) What are the most important soil properties contributing to the change on soil microbial biomass abundance in the passive restoration process? Our results showed that, in some biomes, the levels of soil properties, microbial biomass, and bacterial communities increased during the passive restoration process, but, even if the factors driving forest degradation are removed, the soil may not return to its original state. Moreover, we found that there are only moderate correlations between microbial C and N response ratios (RR) and SOC RR, in this restoration process.

Keywords: passive restoration, soil microbial biomass, soil bacterial community, soil physical-chemical properties.

Resumen

La restauración pasiva es una estrategia común para la recuperación de la estructura y funcionalidad de los bosques en todo el mundo. El grado en que esto ha ocurrido generalmente se evalúa mediante el estudio de las especies vegetales y animales presentes y las propiedades del suelo, mientras que se ha prestado poca atención a los cambios en las comunidades de microorganismos del suelo. Con el fin de dilucidar la influencia de la restauración pasiva sobre las comunidades de bacterias, la biomasa microbiana y las propiedades físicas y químicas del suelo, en diferentes biomas terrestres, el presente estudio realizó un metaanálisis de 82 artículos para responder a las siguientes preguntas: (i) ¿La resiliencia del microbiota del suelo y las propiedades físicas y químicas del suelo después de un proceso de restauración pasiva varían entre los biomas terrestres? (ii) ¿Cuáles son los niveles de microbiota del suelo y las propiedades físico-químicas del bosque restaurado en comparación con el bosque primario, dentro de los diferentes biomas? (iii) ¿Cuáles son las propiedades del suelo más importantes que contribuyen al cambio en la abundancia de la biomasa microbiana del suelo en el proceso de restauración pasiva? Los resultados mostraron que, en algunos biomas, los niveles de propiedades del suelo, biomasa microbiana y comunidades bacterianas aumentaron durante el proceso de restauración pasiva, pero, incluso si se eliminan los factores que impulsan la degradación forestal, es posible que el suelo no vuelva a su estado original. Además, se encontró que solo existen correlaciones moderadas entre los índices de respuesta (RR) de C y N microbianos y el RR de SOC, en este proceso de restauración.

Palabras clave: restauración pasiva, biomasa microbiana del suelo, comunidad bacteriana del suelo, propiedades físico-químicas del suelo.

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Effect of passive restoration on soil bacterial communities and factors associated in the major terrestrial biomes

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Abstract

Passive restauration is a common strategy for the recovery of the structure and functionality of forests throughout the world. The degree to which this has occurred is usually evaluated through the study of the plant and animal species present, and soil properties, while little attention has been paid to changes in the communities of soil microorganisms. In order to elucidate the influence of passive restoration in different terrestrial biomes on soil bacteria communities, microbial biomass, and the physical and chemical properties of soil, the present study undertook a meta-analysis of 82 articles to answer the following questions: (i) Does the resilience of soil microbiota and the physical and chemical properties of the soil after of a passive restoration process vary among terrestrial biomes? (ii) What are the levels of soil microbiota and the physical-chemical properties of restored forest compared with primary forest, within the different biomes? (iii) What are the most important soil properties contributing to the change on soil microbial biomass abundance in the passive restoration process? Our results showed that, in some biomes, the levels of soil properties, microbial biomass, and bacterial communities increased during the passive restoration process, but, even if the factors driving forest degradation are removed, the soil may not return to its original state. Moreover, we found that there are only moderate correlations between microbial C and N response ratios (RR) and SOC RR, in this restoration process.

1. Introduction

Land-use changes are the main causes of the loss of biodiversity and the structure of terrestrial ecosystems (Nepstad et al., 1999; Asner et al., 2009; Gibbs et al., 2010; Köhl et al., 2015). Restoration is an important strategy to recover the structure and functionality of ecosystems after disturbance (Benayas et al., 2009; Bullock et al., 2011) and passive restoration has been shown to be effective in the recovery of abandoned agricultural lands throughout the world (Cramer et al., 2008; Guariguata and Ostertag, 2011; Shimamoto et al., 2018), with benefits including maximizing biodiversity, provision of ecosystem services, landscape connectivity, and improving soil quality (Zhang, et al., 2011: Crouzeilles et al., 2015). Assessment of the effectiveness of passive restoration to return an ecosystem to its original state has been mainly based on the study of plants, animals, and soil properties (Liu, 2003; Long, 2014; Chazdon and Guariguata, 2016; Deng et al., 2017; Meli et al., 2017). Its ability to restore communities of soil microorganisms, however, has received little attention and is still uncertain.

Microbial biomass and community structure are vital in mediating biogeochemical cycles. Indeed, microbial biomass is the most active fraction of the soil organic matter. Bacteria are the major natural agents responsible for nitrogen fixation and transformation in forest ecosystems (Reed et al, 2011) and are considered to be highly important in decomposing dead fungal biomass and thus incorporate cellulose-derived organic matter into the soil (Štursová et al, 2012; Eichorst and Kuske, 2012; Brabcová et al. 2016; López-Mondéjar et al. 2016). Within the domain Bacteria, the phylums Proteobacteria (copiotrophic), Actinobacteria (copiotrophic) and Acidobacteria (oligotrophic) play a vital role in the carbon cycle and have a function in recovering soils as beneficial to soil nutrient cycling (Aislabie et al., 2013; Fierer et al., 2007; Huang et al., 2015; Kielak et al., 2016).

Therefore, understanding the changes in the soil microbial biomass and bacterial communities during passive restoration activity is essential to our comprehension of forests' responses to perturbations and restoration activities. It is currently understood that changes in soil microbial communities during secondary succession are influenced by several factors, such as pH, concentrations of carbon (C), nitrogen (N), and phosphorus (P)

(Fierer and Jackson, 2006; Banning et al., 2011), land-use history (Jangid et al, 2011), and plant-microbe interactions (Tarlera et al., 2008). These also vary across different spatial scales and ecosystems (Fierer and Jackson, 2006; Tripathi et al., 2016; Zeng et al, 2017; Cai et al., 2018).

Previous global analyses have examined changes in microbial communities and soil properties, according to types of disturbance, methods of restoration, types of ecosystems, and the state secondary succession (Zhao, et al., 2019, Zhou, 2020). For example, Zhao, et al., (2019) developed a global meta-analysis and found that soil microbial biomass, and soil bacterial and fungal abundance increased during the first 10 years, but decreased beyond 30 years. Zhou, et al., (2017) showed that the proportion of fungi to bacteria was significantly higher in forest than in grasslands and Zhou et al. (2018) found a significant correlation between microbial C:N ratio and soil pH and C: N. Nonetheless, these studies did not distinguish between primary forests and restored forests, which is key to understanding the stability and resilience of terrestrial ecosystems.

This meta-analysis aims to elucidate the influence of secondary succession on soil bacteria communities, microbial biomass, and the physical and chemical properties of the soil, in different terrestrial biomes. Thus, the following questions were addressed: (i) Does the resilience of soil microbiota and the physical and chemical properties of the soil after of a passive restauration process vary among terrestrial biomes? (ii) What are the levels of soil microbiota and the physical-chemical properties of restored forests compared with primary forest, within the different biomes? (iii) What are the most important soil properties contributing to the change on soil microbial biomass abundance in the passive restoration process? The goal is to contribute to understanding the responses of soil properties, microbial biomass, and soil bacterial communities to the passive restoration process, beyond the microhabitat scale, and the degree to which forest soils can recover after disturbance. This research will also provide information on soil bacterial communities' stability and resilience in major terrestrial biomes.

2. Materials and methods

2.1. Searching literature and data extraction

2.1.1. Literature search

We conducted an extensive literature survey through the ISI Web of Science and Google Scholar, using the following search term combinations: secondary succession, succession forest, restored and primary forest, natural succession, following agricultural abandonment, cropland, secondary forest regeneration, chrono sequence forest and soil microbial, microbial community, microbial biomass, soil bacterial and soil microorganisms.

We looked for the following variables: (a) soil properties, including soil pH, soil organic carbon (SOC), soil total nitrogen (TN) and soil carbon to nitrogen ratio (C:N ratio); (b) microbial biomass properties, namely microbial biomass carbon (MBC), microbial biomass nitrogen (MBN) and microbial C:N ratio (microbial C:N); (c) and six variables representing bacterial community compositions: relative abundances of Acidobacteria (AcidoB), Actinobacteria (ActinoB) and Proteobacteria (ProteoB), in the studies that met the following criteria:

Selection criteria:

- 30-45-year-old forests whit passive restoration (restored forest) that were recovering from farmland or logging (degraded lands), with comparable data from forest in which no disturbance has ever been reported (primary forest), in the same abiotic and biotic conditions.
- Data of the chosen variables (means, observation numbers, and standard deviations or standard error), reported directly in the papers assessed.
- Data of the A horizon or a topsoil layer (0–10, or 0–15 cm), no others.
- Restored forests reported in the same article but with different environmental variables (e.g. passive restoration conducted under several geographical locations), were considered as independent studies.

2.1.2. Data extraction

- We mapped location of studies using QGIS 10.2.
- We chose the Terrestrial Biomes represented at least by three data points in each analysis variable (n > 3).
- We digitized figures with means and errors using PlotDigitizer 2.6.2 (http://plotdigitizer.sourceforge.net).
- We transformed standard errors (SEs) to SDs, when necessary, using the formula: SD = SE (n1/2).

We included 82 papers in this synthesis (Appendix), 39 grouped in “Degraded lands vs. Restored forest”, and 43 in “Primary forest vs. Restored forest”. These papers represent three terrestrial biomes: Temperate broadleaf & mixed forest, Tropical & subtropical moist broadleaf forest, and Montane grasslands & shrublands, adapted from Olson et al. (2001).

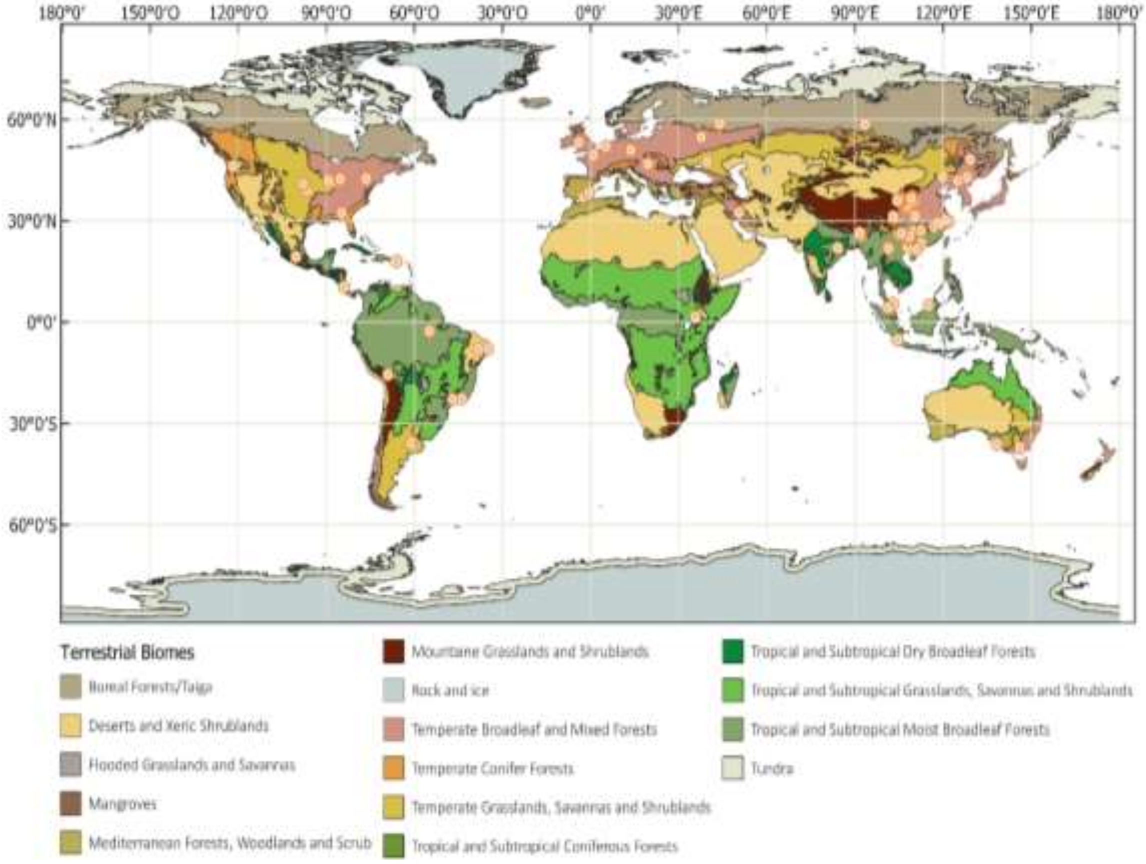

Figure 1. Spatial distribution of the present meta-analysis carried out on a global scale for the period 1997-2020.

2.2. Meta-analysis

2.2.1 Response ratios

We used the response ratio (RR) (Gurevitch and Hedges, 1999; Hedges et al., 1999) to determine the effect of secondary succession (data: Degraded lands vs. Restored forest) and forest degradation (data: Primary forest vs. Restored forest) on which variable, and calculated by Eq. (1).

$$\ln \mathrm{RR} = \ln\left(\frac{X_e}{X_c}\right) \qquad (1)$$

Where Xe and Xc are the means of the concerned variable in the experimental group (restored forest) and control group (degraded lands or primary forest) respectively. We calculated the variance (v) associated with each lnRR using the means, replicate numbers, and SDs of both experimental and control groups.

Because we considered subgroups (terrestrial biome types) in the meta-analysis and these subgroups were not randomly chosen, but represent fixed levels of a chosen characteristic to assess (Borenstein and Higgins 2013), we employed a fixed-effects-model and calculated the weighted mean of the natural logarithm of the response ratio (ln RR++) (Eq. 2).

$$\ln RR_{++} = \frac{\sum_{i=1}^{k} w_i \ \ln RR}{\sum_{i=1}^{k} w_i} \qquad (2)$$

where k is the number of observations and w is the equals the reciprocal of the variance (1/v).

Also, we transformed the lnRR++ into the change percentage (A) to estimates the recovery percentage of the analyzed variables in the passive restoration process (Degraded land vs. Restored forest), and the percentage changes of the same variables concerning reference forest (Primary forest vs. Restored forest) (Eq. 3).

The recovery effect was considered significant when the confidence interval (CI) of the change percentage at the 95% level did not overlap with zero, (Koricheva et al., 2013).

$$A = \left(e^{\ln RR_{++}} - 1\right) \times 100\% \qquad (3)$$

Therefore, in this meta-analysis, A+ represents a result that favors the experimental group (restored forest), while A- shows a result that favors the control group (degraded lands or primary forest).

2.2.2. Subgroup analysis and publication bias

We identified whether microbial biomass, bacterial community composition and soil properties change percentages differed among the subgroup (terrestrial biomes) by using a one-way analysis of variance (ANOVA or MetaAnova). Then, we estimated a linear regression analysis to examine the relationships between the RRs of microbial biomass and the RRs of soil properties for the two data: “Degraded lands vs. Restored forest” and “Primary forest vs. Restored forest”. We used the Egger test to check for publication bias (p 0.01).

Meta-analysis was conducted with Rstudio software.

3. Results

3.1. Effect of passive restoration on soil microbial biomass, bacterial communities and soil properties recovery

Degraded lands vs. Restored forest

Microbial biomass, bacterial diversity, and soil properties levels were greater in restored forest than in degraded lands (Figure 2). Subgroup analysis and ANOVA revealed that microbial biomass carbon increments, as an effect of passive restoration, were different among the three biomes ($p<0.05$), in the following descending order: temperate broadleaf & mixed forest (29%); tropical & subtropical moist broadleaf forest (11%); montane grasslands & shrublands (4%). Microbial biomass nitrogen, microbial C:N ratio, bacterial communities and soil properties were only analyzed for temperate broadleaf and mixed forest, due to the lack of published data for other biomes.

Within bacterial phyla, forest restoration consistently increased the relative abundances of Acidobacteria, Actinobacteria, and Proteobacteria in the temperate broadleaf and mixed forest (<40%) (Figure 2). Moreover, restored forest of temperate broadleaf and mixed biome had 70% more SOC, 70% more TN, 60% greater C: N, and 37% higher pH than comparable degraded lands. Similarly, the passive restoration of montane grasslands and shrublands biome also increased soil TN amount (60%) (Figure 3).

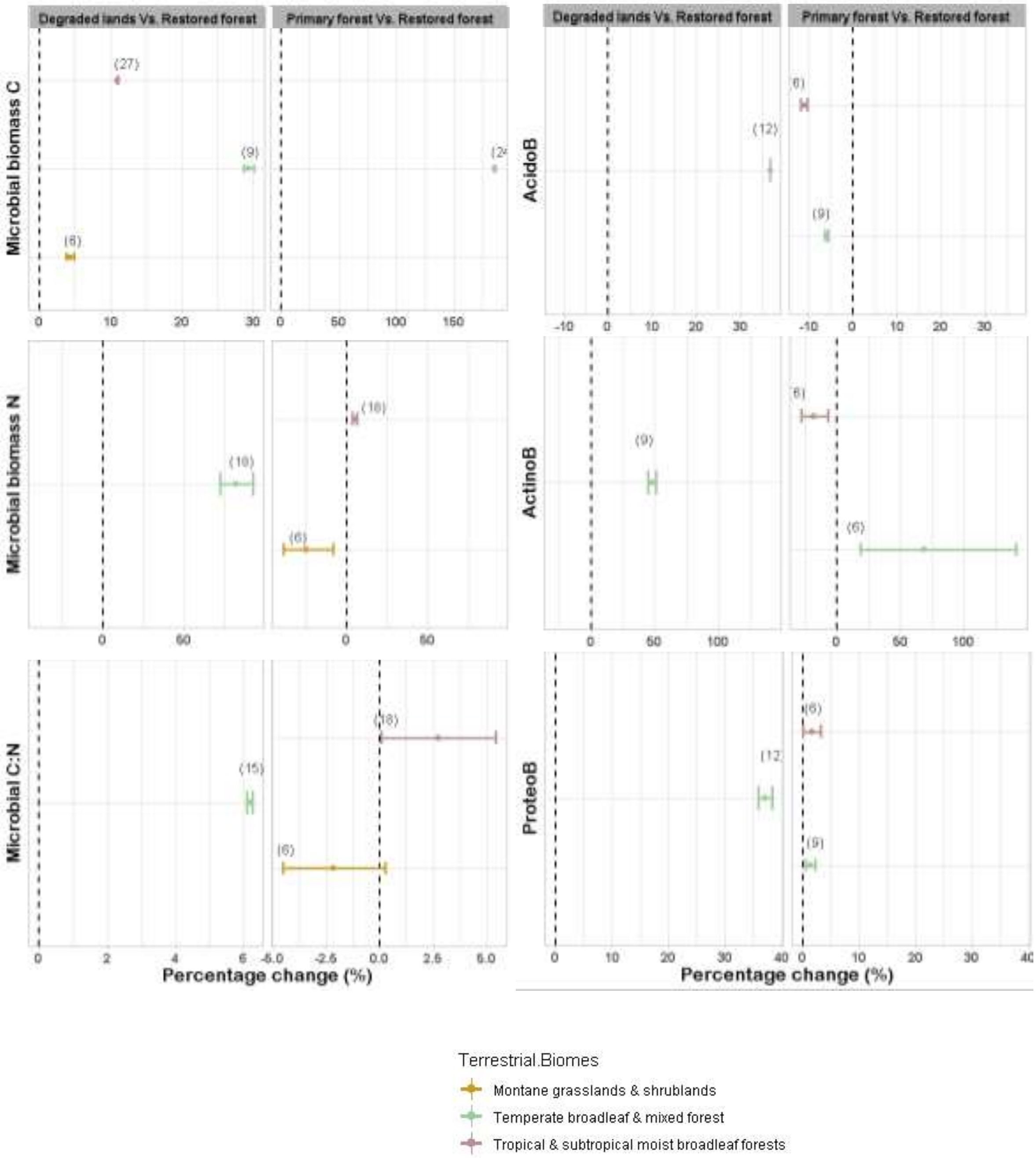

Figure 2. Effects of passive restoration on microbial composition (Microbial biomass C: microbial biomass carbon, Microbial biomass N: microbial biomass nitrogen and Microbial C: N: microbial C:N ratio), and bacterial community (AdcidoB: Acidobacteria, ActinoB: Actinobacteria, ProteoB: Proteobacteria) with respect to degraded lands (Degraded lands Vs. Restored forest) and reference forest (Primary forest Vs. Restored forest). The bars represent the 95% confidence intervals (CIs). The vertical dashed lines are the reference of a response ratio of zero and the numbers in parentheses are sample sizes.

Primary forest vs. Restored forest

Microbial biomass carbon was higher in restored forest when compared to primary forest in temperate broadleaf and mixed forest biome (Figure 2). In contrast, microbial biomass nitrogen was 25% lower in restored montane grasslands and shrublands soils, while in tropical and subtropical forests the soil microbial biomass differences between primary forest and restored forest were not significantly different ($p>0.05$) (Figure 2). On the other hand, Acidobacteria and Proteobacteria showed about 10% more in primary forest, compared to restored forest in temperate broadleaf and mixed forest, and tropical and subtropical forests. Conversely, Actinobacteria abundance depended on the biome ($p<0.001$), with 20% fewer in restored tropical and subtropical moist broadleaf forests, but 75% more in restored temperate forests, compared to examples of primary forest. Additionally, in the comparison of primary forest and restored forest, the metaANOVA showed that SOC and soil C: N levels were also influenced by biome type ($p<0.05$) (Figure 3). On the other hand, soil pH did not differ significantly between primary forest and restored forest (<3%).

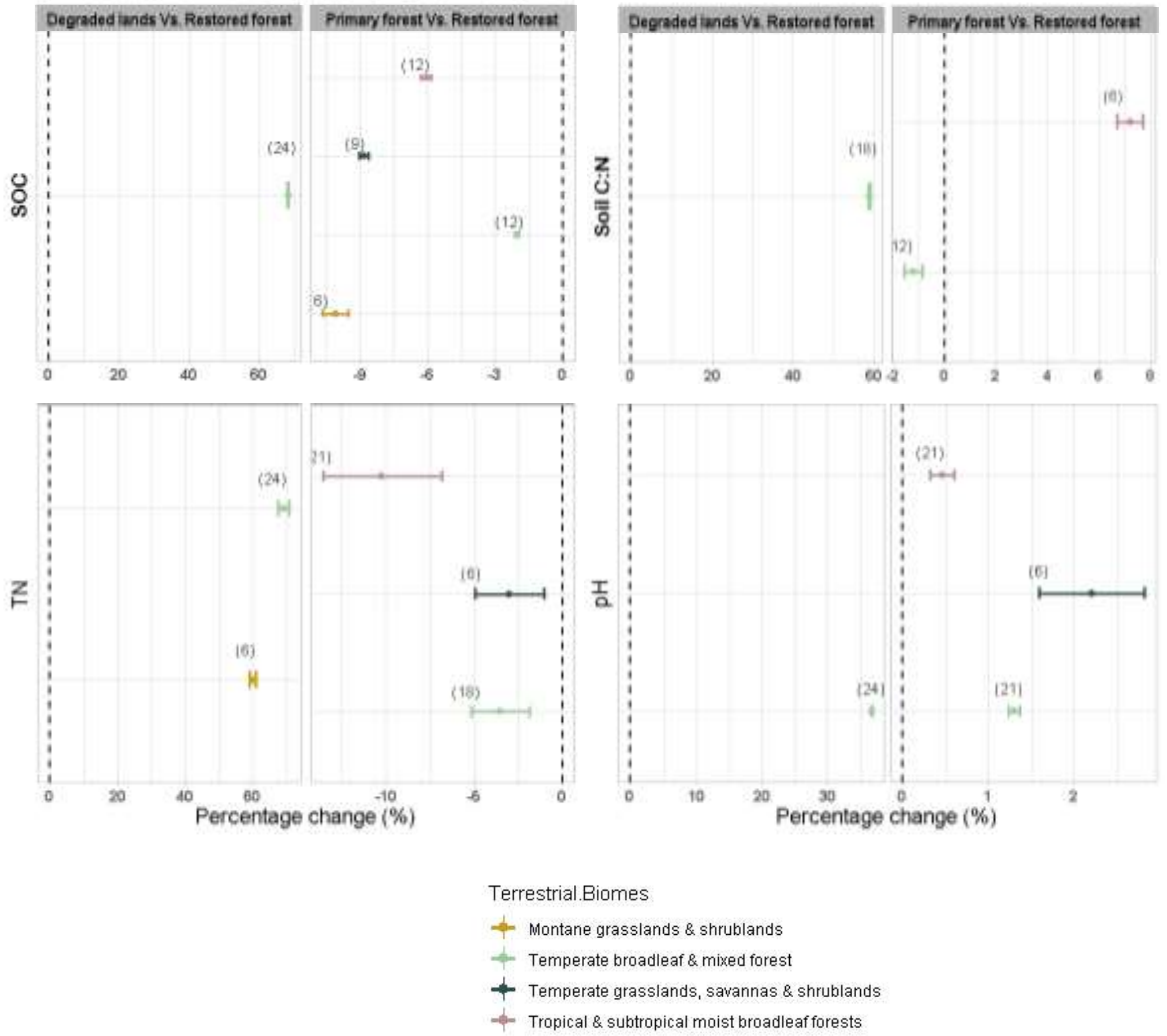

Figure 3.- Effects of passive restoration on soil properties (Soil N: soil nitrogen; SOC: soil organic carbon; soil C: N: soil carbon to nitrogen ratio) with respect to degraded lands (Degraded lands Vs. Restored forest) and reference forest (Primary forest Vs. Restored forest). The bars represent the 95% confidence intervals (CIs). The vertical dashed lines are the reference of a response ratio of zero and the numbers in parentheses are sample sizes

3.2. Factors affecting soil microbial biomass in a passive restoration

There were only moderate correlations between microbial C and N response ratios (RR) and SOC RR, in the restored forest from degraded lands (Figure 4). In contrast, microbial C RR between primary forest and restored forest was highly correlated with SOC (R = 0.75, p = 0.03).

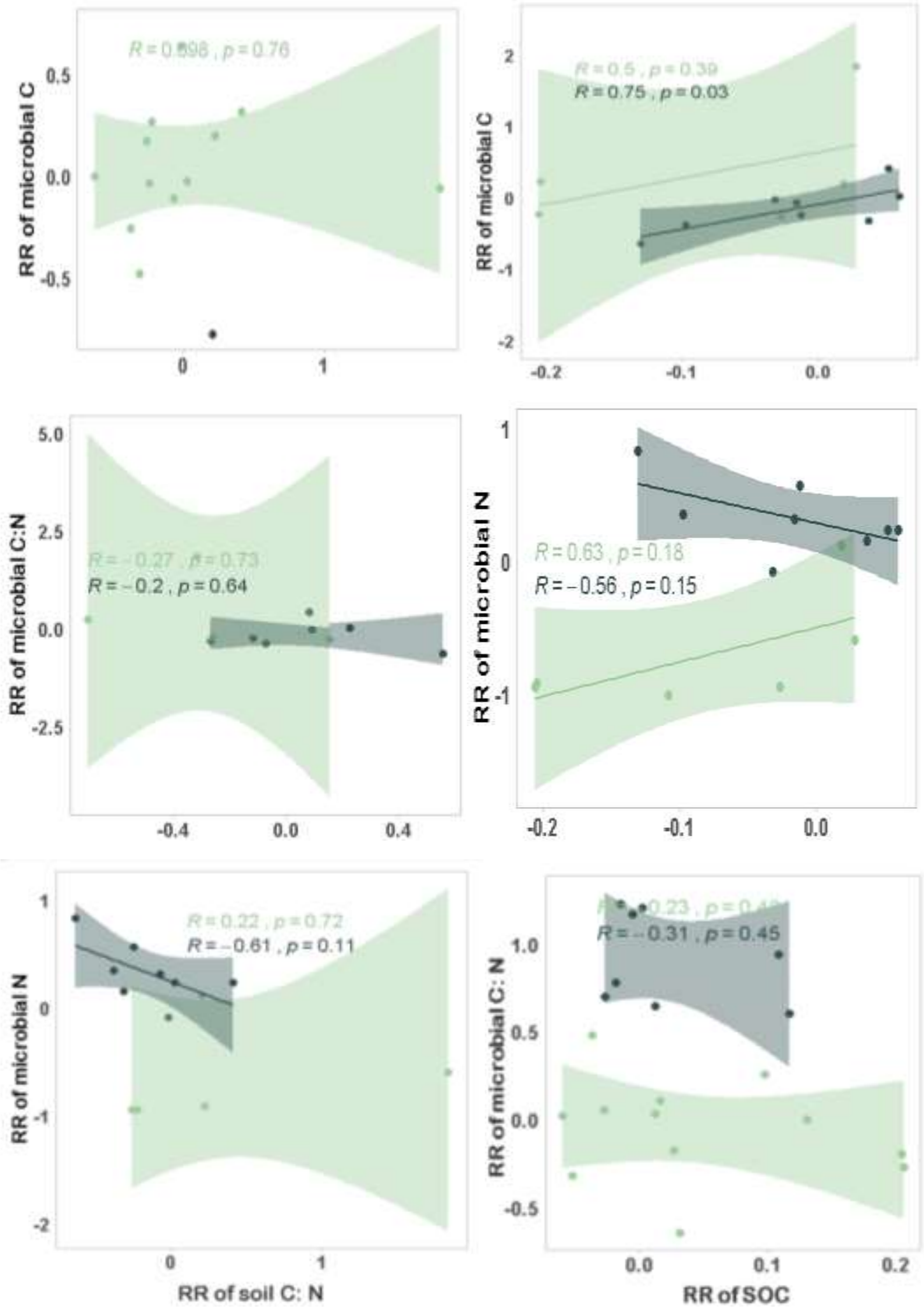

Figure 4.- Relationships between the response ratios (RRs) of soil properties (soil C: N: soil C:N ratio; SOC: soil organic carbon) and the RRs of microbial composition (microbial C: microbial biomass carbon; microbial N: microbial biomass nitrogen; microbial C: N: microbial C:N ratio). Gray color: Primary forest vs. Restored forest; Green color: Degraded lands vs. Restored forest.

4. Discussion

4.1. Effect of passive restoration on soil microbial biomass, bacterial communities and soil properties recovery.

We found that the microbial biomass, soil bacterial communities and soil properties were affected by the passive restoration process (Figure 2). Compared with degraded lands (farmland or logging), soils of restored forest were significantly richer, which was consistent with other meta-analyses conducted at the global scale (Fierer et al., 2009; Lange et al., 2015; Khlifa et al., 2017; Chen et al., 2019). Furthermore, we also found that increases in microbial biomass, soil bacterial communities and soil properties during regeneration depends on the geographic location of the restored soil. Thus, the trend for microbial biomass to return to natural levels also may depend on the biome analyzed (Figure 2).
Our analysis showed that passive restoration successfully recovers the relative abundance of Acidobacteria, Actinobacteria, and Proteobacteria (Figure 2). Previous research suggested that there are competitive interactions between copiotrophs (Proteobacteria) and oligotrophs (Actinobacteria and Acidobacteria) during the restoration process (Ramirez et al., 2012; Guo et al., 2018; Chen et al, 2018). However, our results suggest that Acidobacteria, Actinobacteria, and Proteobacteria showed a similar percentage of relative abundance recovery in restored forest. Moreover, this study showed that different biomes influence the magnitude of soil bacterial communities' recovery during regeneration.

4.1.1 Degraded lands vs. Restored forest

Montane grassland and shrublands biome

Microbial biomass carbon recovery in restored forest of 4% compared to degraded lands was not significant in this biome, probably because the number of cases was low and therefore the 95% CI of MBC percentage of change was larger. However, this could be characteristic for this biome. Soil microorganisms of high-elevation ecosystems respond sensitively to changes in land use because low temperatures limit soil development, primary productivity, and nutrient cycling (Körner, 2003; Bühlmann et al., 2011). Moreover, lower MBC recovery could be also associated with the forest revegetation direction, which can be affecting by restoration type (Zhang, et al., 2011; Cao, et al., 2017). Invasive species that are out of balance with the local ecology are a major problem in secondary forests and are usually not controlled in passive restoration (Anderson, 1995), with ecological impacts that range from local suppression of native species to whole-scale changes in the functioning of ecosystems (Mack, 1986; Chornesky and Randall, 2003). For example, the expansion of Green Alder (Alnus viridis) across the Alps is much faster than the re-growth of the primary montane forests there (Anthelme et al., 2007; Svensk, et al., 2021), leading to increases in total nitrogen (TN) given that alders fix nitrogen (Figure 3).

Temperate broadleaf and mixed forest

In the restored temperate forest, MBC and MBN level increased by 29% and 85% respectively, compared with degraded lands, which was significantly higher than other biomes (Figure 2). It is probably because the warm weather and humid climate are favorable for regeneration, which provides a positive rhizosphere effect on soil microorganisms (Rutigliano et al., 2004; Singh et al.,2004; Mackay et al., 2016). This enhancement of plant productivity and litter biomass would lead to accumulation of soil organic matter (Figure 3), which is an important substrate for soil microbes (Camenzind et al., 2018; Chen et al., 2018). Also, compared with montane grasslands, the leaf litter here decomposes faster and presents better nutrition (e.g., balanced nitrogen availability) (Kanerva and Smolander, 2007). In addition, our study demonstrated an increase in pH in response to passive restoration process, which is important because lead to changes in the microbial community (Fierer and Jackson, 2006; Rosenzweig et al., 2016).

The abundance of different bacteria phyla varied in the restored forest soil in this biome and there were differences between these and those of degraded lands. Proteobacteria are known to be copiotrophic, and their presence correlates positively with C and N pools (Goldfarb et al., 2011; Zhang et al., 2016), while both Actinobacteria and Acidobacteria are often considered oligotrophs and are adapted to resource-limited conditions (Fierer et al., 2007). Interestingly, there are not significant differences between the percentages of recovery of Acidobacteria and Proteobacteria, which may suggest that late-state restored forests do not show a distinction between the recovery of copiotrophic groups and oligotrophic groups in this biome.

Tropical and subtropical moist broadleaf forest

The present meta-analysis showed only small amounts of microbial biomass in soils of restored forests. Although the researchers found for this biome has focused mainly on MBC, this difference might be because soils in the (sub) tropical forests can be highly weathered and depleted in phosphorus, and constrain the accumulation of organic C, which can limit soil microbial growth (Nottingham et al., 2015; Vitousek et al., 2010; He et al., 2020; Miki et al, 2020). Thus, these characteristics prevent a positive correlation between high productivity and microbial biomass (Prach and Walker, 2020). This may also be related to rapid litter decomposition in this warm, moist environment, in which nutrients are assimilated almost immediately by plants (Palm et al., 2007). Although some studies report that plant diversity increases soil microbial biomass across a diverse range of terrestrial ecosystems (Zak et al., 2003; Lange et al. 2015; Chen et al., 2019), our study did not show this relation in the terrestrial biomes.

4.1.2. Primary forest vs. Restored forest

Montane grassland and shrublands biome

MBN level of montane grasslands and shrublands was 25% lower in restored forest, compared primary forest, in contrast to the case of tropical and subtropical moist broadleaf forests. The difference between primary forest and restored forest in microbial biomass C: N levels was only 3% (Figure 2 and 3), suggesting that the passive restoration process does not change the proportion of bacterial to fungal biomass, but does change the capacity of microbial communities to decompose biomass, fix N, and mineralize N (Jia et al., 2005; Guo et al., 2018). Besides, forest regeneration affects the quality of SOM, preventing the availability of C, which was reflected in the SOC level for degraded lands (Figure 3). Although the difference in SOC between primary forest and restored forest is just 10%, it is the highest among the three biomes that were studied. This could be a consequence of burning or grazing, which are factors that significantly influence the accumulation of dead biomass in primary grassland and shrublands (Baer, 2002). Despite this, our results showed the total SOC would be natural regeneration of this biome (Figure 3). This is a promising result since grasslands are important ecosystems for global C and N cycles, considering that they store 10–30% of SOC globally (Follett and Reed, 2010; Qiu et al., 2013).

Temperate broadleaf and mixed forest

MBC level was significantly higher (185%) in restored forests than primary temperate forests. This may be due to the qualities and quantities of primary forest leaf litter, which contains more lignin and nitrogen (Figure 3), ultimately limiting microbial growth (Schipper et al., 2011; Griffiths and Philippot, 2013; Hawkes and Keitt, 2015; Zhang et al., 2016). Nonetheless, the main bacteria phyla relative abundance in the restored forest was similar that of primary forests. This may be due to the fine-textured soils of temperate forests that have silt contents between 50% and 80%, which is more favorable for bacterial growth because they improve the water-holding capacity and nutrient availability, in addition to protecting against bacterial grazers (Xu et al, 2018). Thus, for environmental restoration objectives, our results are encouraging since the major recycling pathways in temperate forests is microbial decomposition (Pausas and Bond, 2020).

Tropical and subtropical moist broadleaf forest

Although there are only a few data to support a trend of MBC recovery back to levels found in primary forest, our results showed similar MBN, microbial C: N ratio, SOC and TN, Acidobacteria, Actinobacteria, and Proteobacteria abundance in the restored and primary tropical forests (Figure 3 and 4). Tropical/subtropical forest soil property recovery could be due to the structure of these forests. For instance, trees and other species that inhabit forest canopies (e.g., epiphytes, lianas), together with understory vegetation, may increase soil carbon and nutrient input quantity and quality during passive restoration process (Santiago and Wright, 2007). Furthermore, the recovery of the properties of these soils after a perturbation (e.g., farming) could be easier due to the lower natural levels of nutrients (Xu et al., 2018). The present study confirmed that passive restoration is a viable way to mitigate anthropogenic impacts on tropical forest soils (Deng et al., 2016, Shimamoto et al., 2018), even though a full return to the enormous species richness of these forests will take a long time (Chazdon and Guariguata, 2016).

Our result showed that a passive restoration strategy does contribute to the recovery of the relative abundance of bacteria in the Acidobacteria and Proteobacteria to levels similar to those of primary forest. Actinobacteria, however, do not respond in same way (Figure 2). Curiously, a meta-analysis of bacterial responses to land-use changes across the tropics forest found a consistent decline in Acidobacteria and Proteobacteria and increases in Actinobacteria (Petersen et al., 2019).

4.2. Factors affecting soil microbial biomass in a passive restoration

We found that the response ratios of MBN and microbial C: N did not show correlations with the response ratios of SOC or soil C: N. The response ratio of SOC showed a positive correlation with the response ratio of MBC in degraded lands vs. restored forest, which means that increasing soil C inputs through plant root exudation and litter production may likely stimulate microbial biomass production.

5. Conclusion

Terrestrial biomes show different trends and magnitudes of recovery of microbial biomass, bacterial communities, and physical and chemical soil parameters. In some biomes, passive restoration may partially offset the losses of SOC, TN, soil C: N ratio, and bacterial communities, caused by land degradation. However, removing the human activity that caused the degradation may not necessarily cause the system to revert to its natural state, or recovery could be very slow (> 40 years). This last result may be verified by increasing the microbial diversity component in the present meta-analysis. Finally, new efforts are needed to quantify the effect of restoration on soil bacterial communities and its factors associated with all terrestrial biomes, including primary forests as experimental controls.

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7. Appendix

Supplementary data

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