Contributed Paper

Amazonian deforestation and soil biodiversity

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Abstract: *Clearance and perturbation of Amazonian forests are one of the greatest threats to tropical biodiversity conservation of our times. A better understanding of how soil communities respond to Amazonian deforestation is crucially needed to inform policy interventions that effectively protect biodiversity and the essential ecosystem services it provides. We assessed the impact of deforestation and ecosystem conversion to arable land on Amazonian soil biodiversity through a meta-analysis. We analyzed 274 pairwise comparisons of soil biodiversity in Amazonian primary forests and sites under different stages of deforestation and land-use conversion: disturbed (wildfire and selective logging) and slash-and-burnt forests, pastures, and cropping systems. Overall, 60% and 51% of responses of soil macrofauna and microbial community attributes (i.e., abundance, biomass, richness, and diversity indexes) to deforestation were negative, respectively. We found few studies on mesofauna (e.g., microarthropods) and microfauna (e.g., protozoa and nematodes), so those groups could not be analyzed. Macrofauna abundance and biomass were more vulnerable to the displacement of forests by pastures than by agricultural fields, whereas microbes showed the opposite pattern. Effects of Amazonian deforestation on macrofauna were more detrimental at sites with mean annual precipitation >1900 mm, and higher losses of microbes occurred in highly acidic soils (pH < 4.5). Limited geographic coverage, omission of meso- and microfauna, and low taxonomic resolution were main factors impairing generalizations from the data set. Few studies assessed the impacts of within-forest disturbance (wildfires and selective logging) on soil species in Amazonia, where logging operations rapidly expand across public lands and more frequent severe dry seasons are increasing the prevalence of wildfires.*

Keywords: land-use change, meta-analysis, microorganisms, rainforest, soil fauna

Deforestación en el Amazonas y Biodiversidad del Suelo

Resumen: *Actualmente, el despeje y la perturbación de los bosques del Amazonas son las principales amenazas para la conservación de la biodiversidad tropical. Se requiere urgentemente de un mejor entendimiento sobre cómo las comunidades del suelo responden a la deforestación amazónica para informar a las intervenciones políticas que protegen efectivamente a la biodiversidad y a los servicios ambientales esenciales que proporciona. Evaluamos el impacto de la deforestación y la conversión del ecosistema a suelo arable sobre la biodiversidad del suelo amazónico por medio de un meta-análisis. Analizamos 274 comparaciones por pares de la biodiversidad del suelo amazónico en bosques primarios y sitios bajo diferentes etapas de deforestación y conversión de uso de suelo: bosques perturbados (incendios forestales y tala selectiva) y de corte-y-quema, pasturas, y sistemas agrícolas. En general, el 60% y el 51% de las respuestas de los atributos (es decir, abundancia, biomasa, riqueza, e índices de biodiversidad) de la macrofauna del suelo y de las comunidades microbianas ante la deforestación fueron negativas, respectivamente. Encontramos pocos estudios sobre la mesofauna (p. ej.: microartrópodos) y la microfauna (p. ej.: protozoarios y nematodos), así que estos grupos no pudieron ser analizados. La abundancia de la macrofauna y la biomasa fueron más vulnerables al desplazamiento de bosques por las pasturas que por los campos agrícolas, mientras que los microbios mostraron el patrón opuesto. Los efectos de la deforestación amazónica sobre la macrofauna fueron más dañinos en sitios con una precipitación anual media mayor a los 1,900 mm, y ocurrieron pérdidas más elevadas de microbios*

en suelos con una acidez alta (pH < 4.5). La cobertura geográfica limitada, la omisión de la mesofauna y la microfauna, y la baja resolución taxonómica fueron los factores principales que obstaculizaron las generalizaciones del conjunto de datos. Pocos estudios evaluaron los impactos de las perturbaciones internas del bosque (incendios forestales y tala selectiva) sobre las especies del suelo amazónico, a la vez que las operaciones de tala se expanden rápidamente en los terrenos públicos y la ocurrencia con mayor frecuencia de temporadas con sequía grave aumentan la prevalencia de los incendios forestales.

Palabras Clave: cambio de uso de suelo, fauna del suelo, meta-análisis, microorganismos, selva

摘要： 对亚马逊森林的砍伐和干扰是当今热带生物多样性保护面临的最大威胁之一。为制定有效保护生物多样性及其提供的基础生态系统服务的干预政策, 目前迫切需要更好地理解土壤生物群落如何响应亚马逊森林砍伐。我们通过荟萃分析, 评估了森林砍伐及生态系统向耕地的转化对亚马逊土壤生物多样性的影响。我们对亚马逊的原生林和森林砍伐或土地利用转化不同阶段的位点 (有野火或择伐干扰的森林、刀耕火种的森林、牧场、耕种系统) 的土壤生物多样性进行了 274 对数据比较分析。总体上, 土壤大型动物群和微生物群落特征 (即丰度、生物量、丰富度和多样性指数) 对森林砍伐的响应分别有 60% 和 51% 为负面响应。我们发现对中型动物群 (如微小节肢动物) 和小型动物群 (如原生动物和线虫) 的研究很少, 因此无法对这些类群进行分析。相比于农业用地取代森林, 大型动物群的丰度和生物量对于牧场对森林的取代更为敏感, 而微生物则相反。在年平均降水量超过 1,900 毫米的位点, 亚马逊森林砍伐对大型动物群的有害影响更大; 而在酸性强的土壤 (pH < 4.5) 中, 微生物的丧失更严重。该数据集的普适化面临的主要问题是其地理覆盖有限、中小型动物群数据缺失和系统分类解析度低。很少有研究评估亚马逊森林内部干扰 (野火和择伐) 对土壤物种的影响, 而择伐作业正在公共土地上快速扩张, 且愈加频繁的严重旱季正在增加野火的发生。【翻译: 胡怡思; 审校: 聂永刚】

关键词： 土地利用变化, 土壤动物群, 微生物, 荟萃分析, 雨林

Introduction

In tropical regions, which harbor hyperdiverse forest ecosystems (Basset et al. 2012), the conversion of rainforest to pasture and cropping systems poses a severe threat to biodiversity (Barnes et al. 2017). Tropical deforestation and ecosystem conversion to arable land removes plant biomass and disturbs soils, resulting in loss of soil carbon and other nutrients and changes in soil properties and biodiversity (Neill et al. 1997; Cerri et al. 2004; Smith et al. 2016). As a result, high-risk areas for biodiversity loss have increased in tropical biomes, including Amazonia (Laurance et al. 2000; Betts et al. 2017), the largest reservoir of terrestrial biodiversity on Earth. Recent studies in Amazonian rainforests show that responses of belowground biodiversity to deforestation, although understudied, can be remarkably different from those of aboveground plants and animals. For example, the conversion of Amazonian forests to cattle pasture reduces the number of plant and animal species (Dale et al. 1994; Gibson et al. 2011), whereas soil microbial diversity appears to increase locally (Jesus et al. 2009; de Carvalho et al. 2016), but the loss of endemic microbial species results in homogenization of soil communities across space (Rodrigues et al. 2013). Also, the rapid proliferation of a single peregrine earthworm species following Amazonian deforestation and pasture establishment can enhance earthworm density and biomass while decreasing species richness (Barros et al. 2002, 2004). A better understanding of how soil communities respond to Amazonian deforestation is crucially needed to inform policy that safeguards biodiversity and the essential ecosystem services it provides.

Soil microbes and animals represent as much as one-quarter of Earth's described biodiversity (Decaëns et al. 2006), and environmental changes that alter their abundance and community composition can shift the soil and ecosystem carbon and energy and nutrient flows (Bardgett & Van Der Putten 2014). Soil organisms control almost all aspects of terrestrial organic matter turnover and nutrient cycling (Wall et al. 2008; Wagg et al. 2014) and therefore are important for agricultural production. They regulate the availability of water to plants and the susceptibility of soil to erosion through their influence on soil physical structure (Lavelle et al. 2006; Lehmann et al. 2017). They are major contributors to greenhouse gas emissions and carbon cycling, so an imbalance in their activities affects the global climate (Lubbers et al. 2013; Filser et al. 2016). Soil biodiversity is the source of many important medicines, including antibiotics, and can suppress disease-causing soil organisms and provide clean air, water, and food (Wall et al. 2015). Despite the importance of soil to life aboveground, in Amazonia it was not until 2002 that a major global research initiative funded by the UN Environment Programme (UNEP) and executed by the Tropical Soil Biology and Fertility Institute (TSBF-CIAT) addressed the state of the biome's soil biological diversity (Moreira et al. 2006). The growing body of studies from this and other projects offers an opportunity for data integration and quantitative analysis of soil biodiversity responses with regard to environmental changes at the biome scale.

Amazonian forest cover has declined to about 80% of its original area because of expansion of human land-use change (Fearnside 2005). Although the biome remains the largest intact tropical forest in the world (Lapola

et al. 2014) and despite that much of the land already cleared for farming is poorly used (Bowman et al. 2011), the remaining forests are under increasing threat from deforestation and forest degradation because the Amazonian human population is growing (Davidson et al. 2012). Current patterns of Amazonian forest clearance began with logging of high-value trees, followed by slashing and burning of remaining trees prior to consolidation into large-scale cattle ranching or intensive mechanized agriculture (Lapola et al. 2014). As a result, Amazonia and northern portions of the Cerrado are the only regions in Brazil (about 60% of Amazonia's total area) where pasture area has increased at the expense of native vegetation over the past 20 years (Lapola et al. 2014).

We addressed the effects of Amazonian deforestation on soil biodiversity with a meta-analysis of 274 pairwise comparisons of multiple community attributes of soil biodiversity in Amazonian primary forests and sites under different stages of deforestation and ecosystem conversion. Soil fauna includes detritivores, such as earthworms, millipedes, and dung beetles, herbivores, such as many genera of nematodes and mites, and predators such as spiders and scorpions. The microflora is composed of bacteria, archaea, and fungi. We examined whether Amazonian deforestation increased or decreased the abundance, biomass, taxonomic richness, and diversity indexes of these soil organisms. We expected that the loss of organic matter inputs to soil after deforestation over any period (days immediately after deforestation to years following) would reduce the abundance of decomposers at the base of soil food webs, whereas communities of invertebrates would likely be directly reduced by fire. We also examined controlling effects of environmental site characteristics. We considered gaps in the literature and general implications of our results for future research.

Methods

We synthesized results from local and regional studies of the impacts of deforestation on soil biodiversity across the Amazon Basin. Using ISI Web of Science, we searched for all relevant peer-reviewed articles published prior to August 2017. We searched for keywords *amazon* or *amazonia* (topics) and "*land use*∗*" or "*land cover*∗*" or *deforestation* (topics) and *soil biota* or *belowground organism*∗* or *microb*∗* or *microorganism*∗* or *bacteri*∗* or *fung*∗* or *archaea* or *protozoa*∗* or *mycorrhiz*∗* or *protist*∗* or *fauna* or *invertebrate*∗* or *springtail* or *mite*∗* or *enchytraeid*∗* or *nematod*∗* or *rotifer*∗* or *isopod*∗* or *earthworm*∗* or *termite*∗* or *collembol*∗* or *acari*∗* or *microarthropod*∗* or *macroarthropod*∗* or *microfauna* or *mesofauna* or *macrofauna* or *tardigrad*∗* or *arthropod*∗* or *chilopod*∗* or *diplopod*∗* or *hexapod*∗* or *insect*∗* or *annelid*∗* or *ant*∗*. The same keywords

were searched in Portuguese and Spanish in SciELO, a bibliographic database of Latin-American journals. Combined, the searches on ISI Web of Science and SciELO returned 891 published studies (5,253 studies were returned when all soil terms were omitted). We also asked experts in Amazonian soil biodiversity for nonindexed peer-reviewed publications and searched databases for dissertations and theses. However, we restricted the analysis to published studies that reported or allowed us to calculate changes in means and standard deviations for at least 1 soil taxon due to a specific deforestation scenario and rejected studies if the different land-use types were confounded by different soil types (e.g., as indicated by significant differences in texture) or sampled at different soil depths.

After carefully inspecting 129 preselected publications that included some measure of soil biodiversity, 34 peer-reviewed publications fit our selection criteria for the meta-analysis. From those, we collected information on the deforestation scenario (land-use change, time since deforestation), experimental setup (spatial scale, samples sizes, sampling and measurement method, and edaphoclimatic conditions), and variables assessed (type of soil organisms, community attributes—total abundance, biomass, taxa richness, or diversity indexes). Most papers included multiple taxa, distinct sites, or both. We kept these separate in our analysis if each site had its own forest and deforested treatments. For chronosequences, we used only data from the longest treatments of deforestation in the study. For most studies, sampling occurred during the rainy season because this is when the highest densities, biomass, and taxonomic richness of soil organisms occur (Franklin et al. 2001). Thus, wet-season data were preferred over dry-season data in the few cases where both were presented. If the results were presented graphically, we used PlotDigitizer (http://plotdigitizer.sourceforge.net) to digitize and extract the data.

We identified 4 deforestation scenarios: primary forest converted to disturbed (selective logging or wildfire) primary forests; primary forest converted to deforested site; primary forest converted to pasture; and primary forest converted to agriculture. The first 2 land-use changes represent the early stages of a business-as-usual deforestation, in which primary Amazonian forests are selectively logged prior to the slash-and-burn removal of trees and the establishment of either pastures for cattle ranching or agricultural crops. The integrated studies defined primary forest as natural vegetation without apparent and reported human impacts. Pasture comprises planted grasses but no natural grasslands or savannahs. Agricultural systems reported included perennial crops, such as cocoa, banana, and palm, and annual crops, such as maize and soybean.

We report changes in soil microbes (bacteria, $n = 49$; fungi, $n = 7$; archaea, $n = 4$; undescribed microbes,

$n = 44$) and litter-dwelling and edaphic macrofauna groups (dung beetles, $n = 32$; other coleopterans, $n = 10$; Isoptera, $n = 11$; Diplopoda, $n = 12$; earthworms, $n = 13$; Chilopoda, $n = 12$; Isopoda, $n = 6$; Arachnida, $n = 10$; ants, $n = 16$; other Hymenoptera, $n = 8$; Orthoptera, $n = 8$; Gastropoda, $n = 8$; Homoptera, $n = 6$; Heteroptera, $n = 7$; undescribed macrofauna, $n = 11$) over the Amazon Basin that were the most commonly reported taxa across the synthesized studies.

As a metric of response, we calculated effect sizes based on the natural logarithm of the response ratio (Gurevitch & Hedges 2001): $\ln RR = \ln (D/F)$, where D and F are the means of the variable in the deforested and forested sites, respectively. As typical in meta-analyses, response ratios were weighted by the inverse of the variance to give more weight to studies with larger sample sizes (Gurevitch & Hedges 2001). Effect size >0 indicates positive response to deforestation (i.e., a given community attribute is higher after deforestation). Conversely, effect size <0 indicates negative response to deforestation. Responses are considered significant if the 95% confidence intervals do not overlap 0.

Responses to deforestation were tested in mixed-effect models. Deforestation scenario was a fixed effect, and study was a random effect. Responses of abundance, biomass, taxonomic richness, and diversity indexes to deforestation across all studies were separately analyzed for microbes and macrofauna. A separate model was fit with soil biota grouped into broad trophic groups: microbial decomposers (all microbes), animal decomposers (ants, Chilopoda, Coleoptera, Diplopoda, dung beetle, earthworms, Gastropoda, Isopoda, Isoptera), herbivores (Heteroptera, Homoptera, Orthoptera), and predators (spiders, other Hymenoptera). Because a common objective in meta-analyses is to reveal research gaps, groups of data with fewer than 5 response ratios are presented in the figures, but are not used for quantitative interpretation of results. Separate models were also built to test for potential controlling factors for each taxonomic group with the following predictors: soil and pH; clay, sand, carbon, and nitrogen contents at the control plot (primary forest); mean annual precipitation (MAP); mean annual temperature (MAT); and time since deforestation. Data were fitted with polynomial functions as fixed effects in the models when a predictor had a curvilinear relationship with the response. For each of those models both the marginal R^2 (proportion of variance explained by the moderator variable) and the conditional R^2 (that of the whole model, including the random effect) were calculated following Nakagawa and Schielzeth (2013). All analyses were performed in the R statistical environment (R Core Team 2014) with packages metafor for meta-analytical diagnostics, nlme for model fitting, and piecewiseSEM for obtaining R^2 for mixed-effects models.

Results

Overview of Data Set

We identified 48 suitable experiments from 34 papers that reported impacts of Amazonian deforestation on soil biodiversity (Supporting Information). These studies reported 274 pairwise comparisons from 4 different Amazon deforestation scenarios : primary forest converted to disturbed primary forest ($n = 13$); primary forest converted to deforested site ($n = 17$); primary forest converted to pasture ($n = 141$); and primary forest converted to agriculture ($n = 103$). Among those studies that reported the time since deforestation, 69% of responses were from studies where the deforested treatment was younger than 10 years.

The database covers northern Brazil and southern Colombia; most studies were from Brazil (Fig. 1). A paired-site experimental design and the space-for-time substitution approach were used in all but 1 experiment (Luizão et al. 1999). Macroinvertebrates ($n = 170$) were better represented than microbes ($n = 104$), and no data were included on mesofauna (such as microarthropods) or microfauna (such as protozoa and nematodes) because of insufficient data points. Total abundance ($n = 63$) and biomass ($n = 61$) of soil animals were the most reported variables for macrofauna studies, and microbial biomass was the most common assessed variable for studies on microbes ($n = 42$). Measures of abundance included density of invertebrates, number of gene copies obtained by quantitative polymerase chain reaction, and counts from microbial culture isolation. Biomass metrics included weights of total invertebrates and microbial C and N contents. Studies measured taxonomic richness as number of species per sample or sampling area for
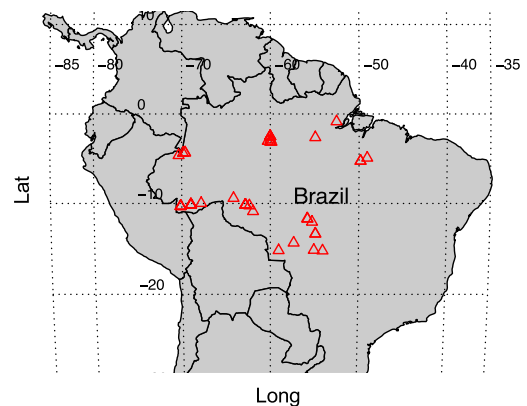

Figure 1. Location of study sites in northern Brazil and southern Colombia that contributed data to a meta-analysis of the effects of Amazonian deforestation on soil biodiversity (grid lines and numbers, latitude and longitude coordinates in degrees).
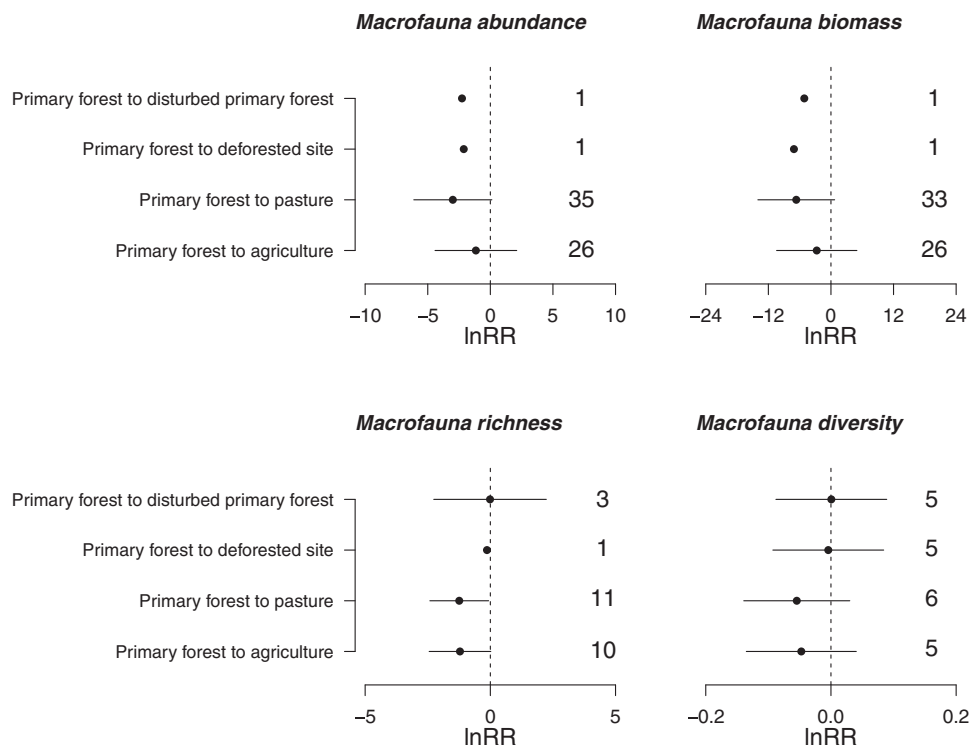
Figure 2. Effects of Amazonian deforestation on soil macrofauna total abundance, total biomass, taxonomic richness, and diversity indexes (whiskers, 95% CI; numbers beside bars, sample sizes). Effect of deforestation is significant if CI of the response ratio (lnRR) does not overlap 0.

invertebrates and as either OTU or gene sequence richness for microbes. Diversity indexes included Shannon index and alpha and beta diversity by Hill's number. The majority of macrofauna studies sampled to 30 cm soil depth ($n = 125$), whereas most microbial surveys were restricted to 10 cm ($n = 64$). Concerning replication, the majority of responses were obtained from 10 replicates or fewer ($n = 193$).

Macrofauna

Deforestation had overall negative effects on soil macrofauna (Fig. 2). The conversion of primary forests to pastures caused a decrease in taxonomic richness accompanied by marginally significant losses of macrofauna abundance and biomass (Fig. 2). Conversion of forests into agricultural systems also tended to negatively affect soil macrofauna, but not significantly (Fig. 2). The effect of different crop systems (e.g., perennial or annual crops) could not be investigated because a very small number of studies covered both deforestation and different crop systems. Macrofauna diversity indexes showed neutral responses to forest disturbance and clearance and nonsignificant negative responses to the establishment of both pasture and agricultural systems (Fig. 2). Overall, 60% of all macrofauna responses to deforestation were negative.

All deforestation scenarios and community attributes combined, macrofauna responses showed a curvilinear relationship with MAP ($p = 0.0001$, $R^2_{marginal} = 30.1\%$, $R^2_{conditional} = 32.2\%$, $n = 118$), reaching a maximum (but

still negative) ratio at around 1900 mm. Soil pH at the primary forest was the only soil attribute to influence macrofauna responses ($p = 0.0187$, $R^2_{marginal} = 8.2\%$, $R^2_{conditional} = 20.3\%$, $n = 63$), but with a shallower negative slope compared to MAP (Fig. 3). The curvilinear relationship between macrofauna response ratios and time since deforestation became negative from the eighth year after deforestation ($p < 0.0001$, $R^2_{marginal} = 61.2\%$, $R^2_{conditional} = 61.2\%$, $n = 41$) (Fig. 3). When modeling the different community attributes separately, MAP and time since deforestation affected macrofauna abundance (MAP: $p = 0.0017$, $R^2_{marginal} = 38.8\%$, $R^2_{conditional} = 38.8\%$, $n = 46$; time since deforestation: $p = 0.0004$, $R^2_{marginal} = 94.1\%$, $R^2_{conditional} = 98.5\%$, $n = 10$), biomass (MAP: $p = 0.0015$, $R^2_{marginal} = 41.7\%$, $R^2_{conditional} = 42.3\%$, $n = 42$; time since deforestation: $p = 0.0004$, $R^2_{marginal} = 94.5\%$, $R^2_{conditional} = 97.9\%$, $n = 9$), and richness (MAP: $p = 0.0816$, $R^2_{marginal} = 18.3\%$, $R^2_{conditional} = 18.3\%$, $n = 25$; time since deforestation: $p = 0.0096$, $R^2_{marginal} = 35.2\%$, $R^2_{conditional} = 35.2\%$, $n = 18$). Response ratios of diversity indexes could not be modeled for environmental controls because the number of replicates was low ($n < 5$). We found no effects of MAT or sand, clay, carbon, and nitrogen content in soil on macrofauna responses.

Microbes

Conversion of forests to agricultural systems had negative effects on microbes that were significant for abundance and nonsignificant for biomass (Fig. 4). Effects of the establishment of pastures on microbes were not statistically
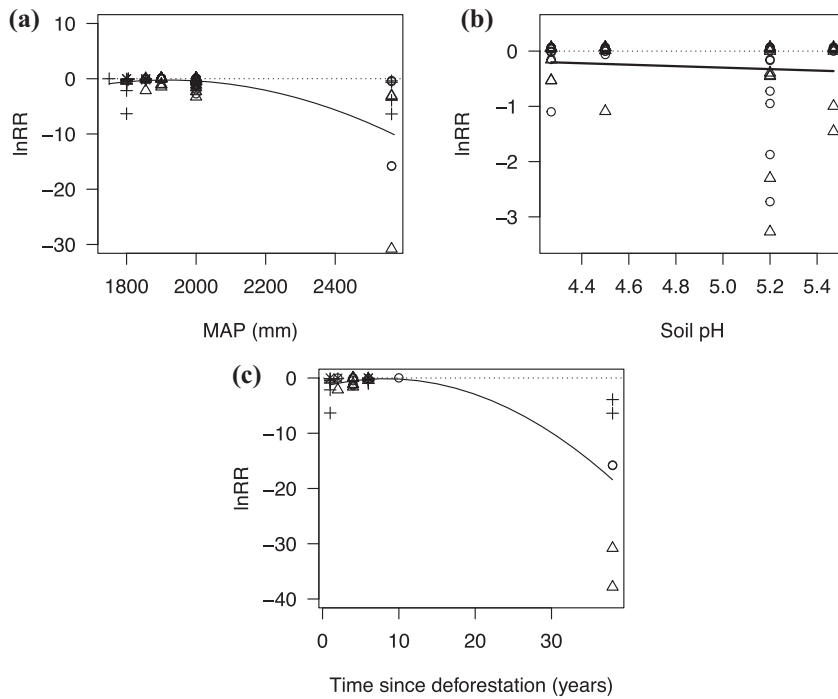
Figure 3. Responses of soil macrofauna to deforestation relative to (a) mean annual precipitation (MAP), (b) soil pH of the primary forest, and (c) time since deforestation (circles, abundance; triangles, biomass; crosses, taxonomic richness; asterisks, diversity indexes; solid line, regression line including all variable classes; dotted line, lnRR = 0).
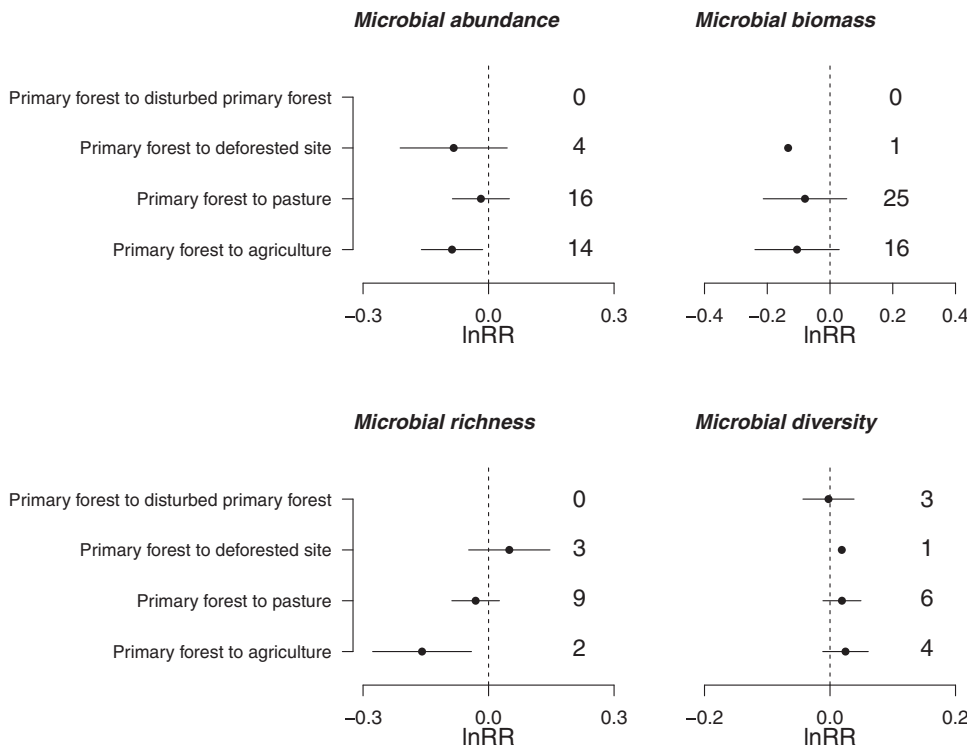

Figure 4. Effects of different types of Amazonian deforestation on soil microbial total abundance, total biomass, taxonomic richness, and diversity indexes (whiskers, 95% CI; numbers beside bars, sample sizes). Effect of deforestation significant if CI of the response ratio (lnRR) does not overlap 0.

supported (Fig. 4). Overall, 51% of all microbial responses to deforestation were negative.

Microbial response ratios increased as soil pH at the primary forest increased, but here statistical support is more uncertain ($p = 0.0932$, $R^2_{\text{marginal}} = 9.9\%$, $R^2_{\text{conditional}}$ = 76.3%, $n = 49$) (Fig. 5). When modeled individually, response ratios for microbial abundance showed a positive relationship with soil pH ($p = 0.0096$, $R^2_{\text{marginal}} = 23.13\%$, $R^2_{\text{conditional}} = 27.78\%$, $n = 32$). Response ratios for microbial biomass were not affected by soil pH, and
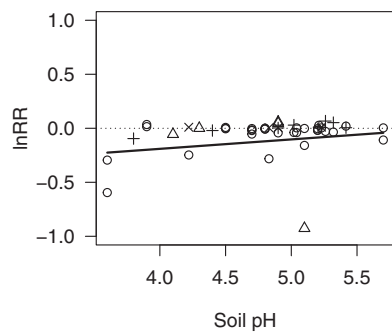
Figure 5. Effects of deforestation on soil microbe relative to soil pH in primary forest (circles, abundance; triangles, biomass; crosses, taxonomic richness; x, diversity indexes; solid line, regression line, including all variable classes; dotted line, lnRR = 0).

response ratios for richness and diversity indexes could not be modeled individually for environmental controls because of the low number of replicates ($n < 5$). Climate conditions and other soil characteristics did not affect microbial responses.

Trophic Groups

The 4 different deforestation scenarios were grouped for the analysis of trophic groups responses because of insufficient data points for the analysis of individual scenarios. The effects of deforestation on the abundance and biomass of predators and herbivores were not statistically supported, although these variables showed consistent tendency to negative responses (Fig. 6). Deforestation also had significant negative effects on the abundance, biomass, and taxa richness of animal decomposers (Fig. 6). Microbial decomposers exhibited neutral responses for its abundance, biomass, richness, and diversity indexes (Fig. 6).

Discussion

Responses of Macrofauna and Microbes to Deforestation

Our results suggest that macrofauna abundance and biomass are more vulnerable to the displacement of forests by pastures than by agricultural fields, whereas microbes showed the opposite pattern (Figs. 2 & 4). Barros et al. (2002) suggest the maintenance of a continuous litter cover at the soil surface in cropping systems may partially prevent macrofauna decreases as compared to those losses observed in western Amazonia pasture soils. In fact, large-scale field surveys in Central Amazon show that deforestation and the establishment of exotic grasses lead to a dramatic fall in total macrofaunal abundance, biomass, and diversity indexes; approximately 70% of the soil macrofaunal taxa of the original forest disappear and

are replaced by large populations of aggressive exotic colonists, such as the earthworm _Pontoscolex corethrurus_, a species that invades many tropical pastures and causes profound soil compaction (Chauvel et al. 1999; Barros et al. 2004).

Stronger responses of microbial communities to the establishment of cropping systems compared to pastures were showed in soil bacteria studies by Lammel et al. (2015) in Brazil and Mantilla-Paredes et al. (2009) in Colombia, although neither study assessed the mechanisms driving such pattern. Contrasting responses of invertebrates and microbes to deforestation were also evident when organisms were grouped according to their trophic function (Fig. 6). The tendency of positive responses for microbial decomposers diversity indexes was consistent with previous empirical evidence that taxonomic and phylogenetic diversity of soil bacteria can increase at local scales after Amazonian deforestation and ecosystem conversion (Jesus et al. 2009; Rodrigues et al. 2013; Mendes et al. 2015; de Carvalho et al. 2016), and soil pH seemed the key driver of such pattern. Tropical soils are naturally acidic, usually requiring pH neutralization through the application of large quantities of lime following conversion of natural habitats to arable land. However, deviations in environmental pH should impose stress to native microorganisms, affecting their growth (Fierer & Jackson 2006; de Carvalho et al. 2016). Thus, the positive effect of soil pH at the control plot (primary forest) on the responses of microbial abundance to deforestation may indicate microbial communities in highly acidic soils (pH < 4.5) are more susceptible after ecosystem conversion due to the high stress imposed by pH neutralization prior to the establishment of arable systems.

Factors Affecting Responses of Soil Biodiversity to Deforestation

Mean annual precipitation negatively influenced macrofauna responses to deforestation in wetter sites (MAP > 1,900 mm) (Fig. 3a). Wet cultivated soils are more prone to soil compaction, and previous research has shown macrofauna avoidance of compacted soils (Radford et al. 2001; Franco et al. 2017). A recent meta-analysis shows greater responses of earthworms to soil tillage disturbance in more humid conditions globally (Briones & Schmidt 2017). Therefore, the recovery of the macrofauna community following deforestation might be encouraged at drier conditions.

Variations in soil pH had only a marginal influence over macrofauna responses compared to either MAP or time since deforestation (Fig. 3). Soil attributes, such as contents of clay, sand, carbon, and nitrogen, did not influence the responses of soil organisms to deforestation. These edaphic characteristics strongly explain the magnitude of deforestation effects on soil microbial communities

Trophic groups abundance

Trophic groups biomass

Trophic groups richness
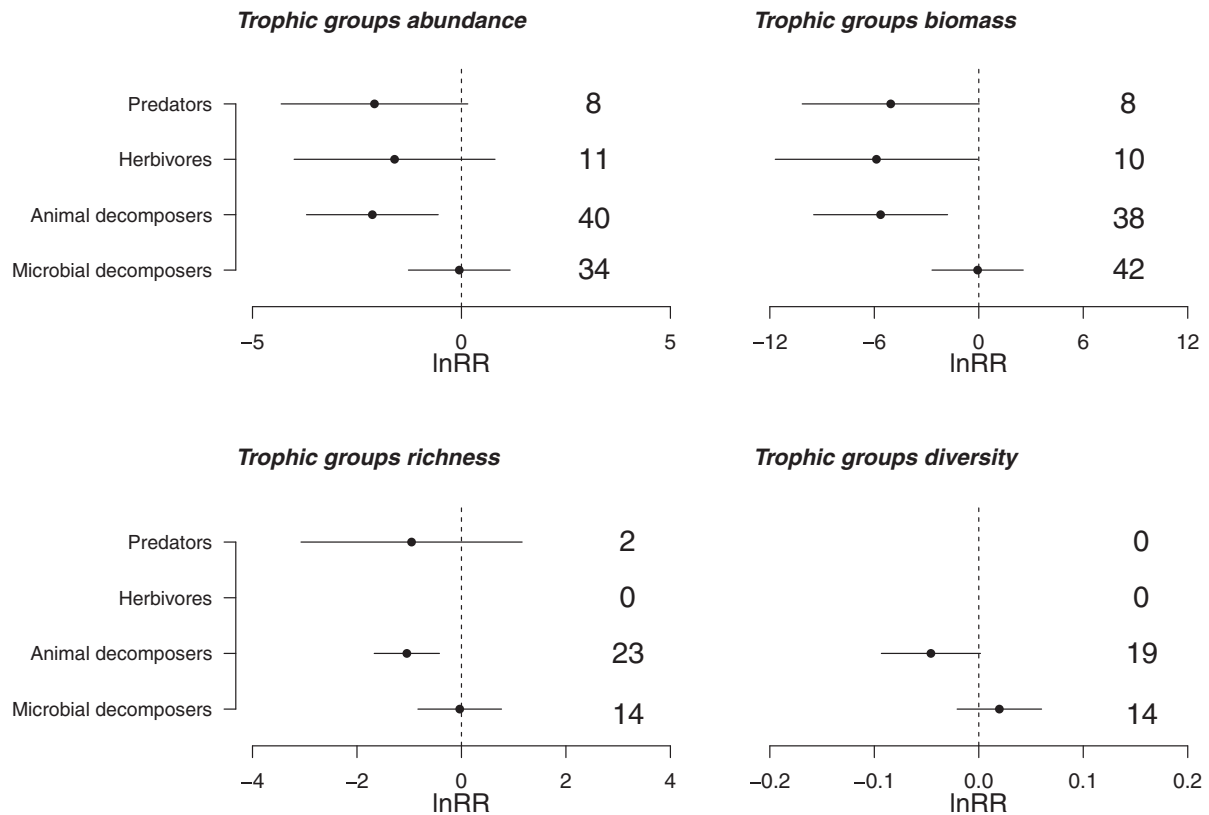

Trophic groups diversity

Figure 6. Effects of Amazonian deforestation on soil-organism trophic group total abundance, total biomass, taxonomic richness, and diversity indexes (solid lines, 95% CI; numbers beside bars, sample sizes). Effect of deforestation on specific trophic groups significant if CI of the response ratio (lnRR) does not overlap 0.

across multiple biomes (Crowther et al. 2014), including Amazonia (Rodrigues et al. 2013), and our results may indicate these attributes were not quantified consistently enough throughout our data set ($n = 35$ for carbon, $n = 24$ for nitrogen, $n = 11$ for both clay and sand contents in microbial studies). The influence of land-use history shown in our results (Fig. 3c) challenges the hypothesis of increasing ability of soil invertebrate communities to adapt to and to recolonize a soil environment that has been repeatedly disturbed over time as the more resilient species would remain (Briones & Schmidt 2017).

Result Implications, Data-Set Limitations, and Research Priorities

Our findings suggest that areas with MAP above 1900 mm would be of high conservation priority for soil invertebrates (Fig. 3a). However, more data are needed before this can be translated into a clear-cut management recommendation for the conservation of soil invertebrates. For example, our database lacked data from areas with MAP ranging from 2000 to 2400 mm and over 2500 mm (MAP in the Amazon basin spans from 1500 to 3000 mm). Our analysis also suggests that microbial communities in highly acidic soils (pH < 4.5) are especially vulnerable

to loss of abundance through deforestation (Fig. 5), but here again results deemed significant should rather be regarded as hypotheses requiring targeted investigation. Although Amazonian soils exhibit pH values from 3.7 to 6.2 (Quesada et al. 2010), most values reported in our database fell in a much narrower range (4.7 and 5.3). Basin-wide variations in Amazonian forest structure and function are mediated by soils and climate (Quesada et al. 2012). Favorable soil fertility is related primarily to soils with relatively low pedogenetic levels near the Andes, and unfavorable fertility conditions are usually associated with soils at an advanced stage of weathering in eastern areas (Quesada et al. 2010). Based on our data set, we could not determine whether this basin-wide heterogeneity affects the resistance or resilience of soil communities to deforestation.

Evidence is mounting that not only deforestation but also most forms of within-forest degradation (e.g. wildfires and selective logging) have a large detrimental effect on tropical biodiversity (Gibson et al. 2011). In Amazonian forests, these forms of disturbance can double biodiversity loss from deforestation (Barlow et al. 2016). However, our meta-analysis revealed a dearth of information on the effects of forest disturbance to Amazonian soil biodiversity (Figs. 2 & 4), and general patterns

could not be drawn. What data are available indicate that wildfires and selective logging can decrease both biomass and species richness of dung beetle communities (França et al. 2016) and decrease diversity of dominant soil bacteria taxa (de Carvalho et al. 2016). We encourage more studies to determine whether anthropogenic action in intact landscapes is in fact disproportionally putting species at most risk of extinction, as recently shown for Amazonian aboveground vertebrates (Betts et al. 2017).

One of the most prominent limitations of the literature in this field is the lack of data from 7 out of the 9 countries that the Amazon biome covers parts of (Bolivia, Peru, Ecuador, Venezuela, Guyana, Suriname and French Guiana) (Fig. 1). Such geographic limitation in our knowledge of deforestation effects on soil biodiversity strongly impairs evidence-based cross-country articulated actions for the protection of biodiversity. Two studies from the Peruvian Amazonia that did not meet the criteria for inclusion in our meta-analysis showed losses of abundance and diversity of litter-dwelling and endogeic macrofauna (Lavelle & Pashanasi 1989; Perry et al. 2016). From a taxonomic point of view, the low number of studies on both soil micro- and mesofauna impairs our ability to predict consequences of deforestation to ecosystem functions maintained by soil biodiversity (Wagg et al. 2014). Among the few studies found that assessed microfauna, Silva et al. (2008) showed increased populations of plant-parasitic nematodes in pasture compared to forest. As for mesofauna, 3 studies consistently reported that increases in the population of Acari Oribatida enhanced mesofauna densities under polyculture plantations compared to primary forests (Franklin et al. 2001; Höfer et al. 2001; Hanagarth et al. 2004), whereas de Morais et al. (2010) found similar taxonomic compositions in cultivated areas compared to primary forest. A prevalent issue in soil ecology is the low taxonomic resolution used in most studies, and this meta-analysis reveals no exception to it. Our trophic group analysis (Fig. 6) would be more accurate if the family or genus identity of the invertebrates and microorganisms had been known, given that groups of fauna and microbes span various trophic levels. Two of the most obvious examples are coleopterans and ants—coleopterans may have very different ecological functions depending on the family and even on whether it is the larval or adult form that is examined, and some species of ants are generalist predators, whereas others, such as leaf-cutter ants (abundant in the tropics), use leaf substrates to grow fungal cultures (Silva & Brandão 2010; Dambros et al. 2016).

Taken together, the results from this meta-analysis suggest that the magnitude of detrimental effects of Amazonian deforestation on soil macrofauna biodiversity increases at wetter sites (MAP > 1900 mm) and that losses of soil microbes after deforestation are greater in highly acidic soils (pH < 4.5). Limited geographic coverage, omission of micro and mesofauna, and low taxonomic resolution used in most studies are main factors impairing generalizations and management recommendations from this literature analysis. Furthermore, the question of how wildfires and selective logging in intact primary forests impact soil species emerges as an important research priority for conserving Amazonian belowground biodiversity. This represents an ample opportunity for soil ecology to offer solid scientific guidance to policy decisions on the protection of biodiversity.

Acknowledgments

Supporting Information

A list of studies included in the database that contributed to the meta-analysis (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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