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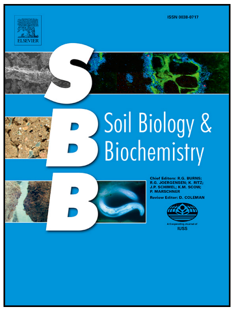

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Title: Earthworms regulate plant productivity and the efficacy of soil fertility amendments in acid soils of the Colombian Llanos

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Abstract

The Llanos region of Colombia represents one of the last large agricultural frontiers and is undergoing a rapid conversion from naturalized savanna to intensive agriculture with high agrochemical inputs and tillage. This massive land-use conversion has considerable impact on ecosystem services and biodiversity, particularly soil macrofauna, yet the full implications of this land-use shift for long-term agroecosystem productivity are poorly understood. To better elucidate potential land-use change impacts on agricultural production we used experimental microcosms in the greenhouse to evaluate how the common earthworm, *Pontoscolex corethrurus*, influences plant growth, nutrient uptake, and key soil properties relative to the application of lime and P fertilizer, both common soil fertility amendments in the region. Additionally, we aimed to explore the potential for interactions between earthworms and these amendments across distinct plant types, the grass *Brachiaria decumbens* and the legume *Phaseolus vulgaris*, which display different rooting patterns and nutrient acquisition strategies. Earthworms increased the biomass production of *B. decumbens* by 180% and N uptake by more than 240%, while P fertilizers and lime additions increased total biomass by less than 30% each for *B. decumbens*. Effects on *P. vulgaris* were similar, but less pronounced with earthworms increasing total biomass production by 35% and total plant N content by 70%, while neither lime nor P alone significantly influenced total biomass or N uptake. However, a significant interaction between earthworms and lime enhanced total biomass N content of *P. vulgaris* by more than 150% relative to microcosms without *P. corethrurus*, suggesting that earthworms can greatly enhance the efficacy of lime in soils. Additionally, we found that earthworms greatly improved soil aggregation, but only in the presence of plants, and that this effect was most prominent in microcosms with *P. vulgaris*. When testing treatment effects on soil P availability, only fertilizer

P additions significantly influenced resin P, but not microbial biomass P. Our findings suggests the importance of developing management strategies that promote the activity and diversity of earthworms and other soil biota as a means to enhance crop productivity, resource use efficiency and a range of soil-based ecosystem services in the Llanos region and beyond.

Key words: *Brachiaria decumbens;* lime; *Phaseolus vulgaris;* phosphorus*; Pontoscolex corethrurus*; soil aggregation

Introduction

Agriculture faces numerous challenges in the coming decades, as increasing demands on food production are often at odds with a need to reduce degradative effects of farming management practices on the environment. To address this issue, farming strategies that use resources more effectively, while minimizing deleterious impacts on biodiversity and the provision of ecosystem services within agricultural lands need to be developed (Foley et al. 2011). The Llanos region of eastern Colombia exemplifies this challenge. As one of the last remaining large agricultural frontiers, this region is being rapidly converted from extensive grazing in semi-natural savanna to intensive, large-scale agriculture (Romero-Ruiz et al. 2012). Due to the low pH and high susceptibility to compaction of the soils in the region, this conversion often relies upon frequent tillage operations and large inputs of fertilizers and lime to develop an arable soil layer (Amezquita et al. 2004). While such interventions are often profitable in the short-term, intensive agriculture, and annual cropping systems in particular (of rice, maize and soy), have been shown to greatly impact soil biological activity and the provision of soil-based ecosystem services in the region, thus threatening the long-term sustainability of these agroecosystems (Decaëns et al. 1994, Lavelle et al. 2014).

A number of studies have focused on the role of soil biological activity and diversity in supporting crop growth and ecosystem services via a range of mechanisms (Barrios 2007). Soil macrofauna, in particular, are known to be important regulators of multiple soil processes and provide sensitive indicators of management impacts on overall soil function (Lavelle et al. 2006, Rousseau et al. 2013). Earthworms are widely recognized to be the most important macrointervebrates in many agricultural soils and have been shown to enhance crop growth in a wide array of farming systems via a variety of mechanisms (Brown et al. 2004, van Groenigen et al. 2014). These mechanisms include increased nutrient availability (especially N and P), enhanced soil aggregation and water availability, as well as improved stress tolerance and pest regulation (Blouin et al. 2005, Lubbers et al. 2011, Andriuzzi et al. 2015). Despite the multiple benefits of earthworms, and whole soil macrofauna communities, to agricultural production, their contributions are often overlooked, with management practices instead focusing on the substitution of key soil biological functions with inputs such as fertilizers and pesticides and management practices like tillage. While studies have documented the beneficial impacts of earthworms and other soil biota on plant growth (van Groenigen et al. 2014), relatively little is known about how earthworms interact with agricultural inputs to support production and the provision of key ecosystem services. For example, Noguera et al. (2010) examined the impacts of earthworms and biochar amendments in two Colombian soils and found there to be a significant positive interaction between these factors for rice production in a relatively poor soil, but not in a more fertile soil. Earthworms have also been shown to facilitate the uptake of fertilizer N and to improve the efficacy of mycorrhizal inoculation in maize-based systems (Fonte and Six 2010, Li et al. 2013). Others have suggested that liming and earthworms are likely to display important interactions with implications for soil aggregation and macroporosity (Haynes and Naidu 1998). While these findings are promising and suggest that earthworms can enhance the efficacy of some soil amendments, little is understood about the relative impacts of earthworms vs. common soil amendments on plant growth and under what conditions synergies are likely to occur.

In order to better understand the potential contribution of earthworms, a prominent driver of soil biological function in soils of the Llanos and globally, we examined their impact on plant growth and nutrient dynamics in a greenhouse setting, along with key soil fertility amendments (lime and P fertilizer) at standard application rates. These effects were tested individually and in all possible combinations across distinct plant types (grass vs. legume vs. grass-legume mixture) to understand how plants with different nutrient acquisition and rooting strategies may determine the relative effectiveness of earthworms vs. soil amendments to enhance crop growth, nutrient uptake and key soil properties. We hypothesized that the relative effect of earthworms on plant growth and nutrient uptake would exceed that of lime and P fertilizer. Additionally, we anticipated positive interactions between earthworms and the soil fertility amendments, such that earthworms enhance the efficacy of these common inputs.

2. Materials and Methods

2.1 Experimental Design

This research was conducted at the International Center for Tropical Agriculture (CIAT) near Cali, Colombia. Earthworms, soil fertility inputs, and plant species were manipulated within microcosms (plastic containers, 17.5 cm dia. × 17 cm tall and fitted 1 mm nylon mesh at the base and on the sides) in a greenhouse. Soil used in this experiment was collected from the 0-20 cm depth in a semi-natural savanna at the Taluma Experimental Station, near Puerto Gaitan, in the Meta Department of Colombia (4° 22' N, 72°13' W). Classified broadly as an Oxisol, and more specifically Typic Hapludox (Camacho-Tamayo et al. 2008), the soil had a pH of 5.15, a C content of 13.5 g C kg^{-1} soil, available P (Bray II) of 2.43 mg kg^{-1}, and a clay-loam texture with 25% sand, 42 % silt and 33% clay. Soil was collected in early 2013 during the dry season and immediately air-dried upon arrival at CIAT. The soil was processed with an industrial mill to pass through a 2 mm sieve, so as to break apart all large macroaggregates. The few stones encountered were removed prior to milling. Soil was mixed with sand at a 3 to 1 ratio (soil to sand ratio) to ensure adequate drainage and aeration, and 2 kg of this mixture was added to each microcosm, where it was gently packed down by hand. The microcosms were watered from below (via capillary action) with deionized water shortly before planting to ensure even wetting of the soils within each microcosm.

Within the microcosms a suite of soil fertility treatments was established, involving the addition or absence P fertilizer, lime, and earthworms in all possible combinations. Additionally, microcosms were planted with one of four plant treatments: 1) *Brachiaria decumbens* alone (a common grass pasture species in the Llanos), common bean (*Phaseolus vulgaris*) alone, a mixture of *B. decumbens* and *P. vulgaris*, and a control that was maintained plant free. The experiment was set up as a full factorial, completely randomized design with 32 treatments and three replicates of each treatment. Seeds of *B. decumbens* were pre-germinated in sand for two weeks prior to transplanting into the microcosms. *P. vulgaris* was seeded directly in the microcosms at the time of the first watering. Based on differences in size and growth rate and to standardize the total biomass, *B. decumbens* was added at a density of four seedlings per microcosm, while *P. vulgaris* was seeded at a rate of two seeds per microcosm. In treatments with a combination of the two plants, two grass seedlings were planted on one side of the microcosm and one bean seeded on the other side. Phosphorus was added to half of the microcosms as super triple phosphate at a rate of 150 mg per microcosm (equivalent to ~50 kg P_2O_5 ha^{-1}, or 22 kg P ha^{-1}) while dolomitic lime was added at a rate of 2.7 g per microcosm (equivalent to 5 Mg ha^{-1}). Both amendments were added prior to the initial watering and thoroughly mixed with the soil to simulate tillage and maximize contact of amendments with soil particles. We note that lime and P are commonly applied in these soils to address issues associated with low-pH, including P deficiency, and the amounts considered here are both within the range of common application rates for intensive pasture and/or cropping systems in the region. Earthworms, of the species *Pontoscolex corethrurus*, were collected from a farm near CIAT, in Palmira, Colombia. Upon collection earthworms were first placed in a petri dish with a moist towel for 48 h to void their guts and ensure the vigor of the individuals used in the experiment. Individuals were rinsed clean, patted dry and weighed, and then applied to half of the microcosms in groups of three, with each group averaging 1.28 g ± 0.05 g total fresh weight. Additions of *P. corethrurus* took place one week after transplanting of the grass seedlings, and once the beans were fully emerged. Earthworm densities (equivalent to roughly 195 individuals m^{-2}) were based on previously observed values for improved pasture systems in the Llanos region and elsewhere (Decaëns et al. 1994, Lavelle et al. 2014). Microcosms were weighed weekly to determine water loss, and water was added as needed to maintain roughly 80% field capacity (determined gravimetrically in a repacked soil-sand mixture) throughout the experiment. Microcosms were maintained until destructive harvest of soil and plant components, 55 days after transplanting.

2.2 Plant Harvest and Analysis

At harvest, plants were cut at the base, and the moist soil was passed through a 10 mm sieve by gently breaking soil clods along natural planes of weakness, and allowed to air-dry prior to subsequent analyses. During this process coarse roots were removed and set aside for washing and drying. Aboveground components were separated into leaves of *B. decumbens*, as well as flowers, pods, leaves, and stems of *P. vulgaris*. Upon washing of the coarse roots, all plant material was oven-dried at 60 °C and weighed. Bean components were recombined to form three vegetative components for nutrient analysis: 1) aboveground biomass of *B. decumbens*, 2) aboveground biomass of *P. vulgaris,* and 3) roots from *B. decumbens* and/or *P. vulgaris*. These different plant components were ground and sent to the CIAT analytical laboratory for determination of total N and P in above and belowground biomass (Jones et al. 1991).

2.3 Soil Processing and Analysis

Following harvest, soil from each microcosm was wet-sieved according to methods adapted from Elliott (1986) to determine treatment impacts on soil aggregation. In brief, 45 g of air-dried soil was placed on top of a 2 mm sieve and submerging the sieve and soil in deionized water for 5 min for slaking. The sieve was moved in and out of the water using an oscillating motion a total of 50 times over a period of 2 min. Soil remaining on the sieve was rinsed into a pre-weighed aluminum pan, while material passing through the sieve was transferred to a 250 µm sieve and the process repeated. This procedure was carried out once more with a 53 µm sieve to yield a total of four size fractions. Aluminum pans for each size fraction were dried in the oven at 60 °C and weighed. The proportion of soil in each size fraction was used to determine mean weight diameter (MWD), a common indicator of aggregate stability, according to the following formula:

$$MWD = \sum_i * P_i S_i$$

where S_i is the average diameter for aggregates in the i^{th} fraction and P_i is the proportion of whole soil found with this fraction (van Bavel 1950).

In order to better understand treatment effects on P availability and soil dynamics both resin P and microbial biomass P were evaluated following Kouno et al. (1995). Previous work in the region suggests that microbial biomass P, in particular, is an important indicator of P turnover and availability in highly weathered and P deficient tropical soils (Oberson et al. 2001). Briefly, this method involves the use of anion-exchange resin strips to assess relatively labile P from soil suspensions containing either soil with distilled water (for determination of resin P) or soil with distilled water and $CHCl_3$ (for microbial biomass P) after 16 h of shaking.

2.4 Statistical Analyses

The influence of the different soil amendments and plant treatments on biomass production and nutrient uptake was analyzed using ANOVA with a full-factorial model considering main effects and all possible interactions of the variables lime, P, and earthworms (each with two levels), and plants (with three treatments considered). Due to significant interactions between plant treatment and the different soil addition treatments, analyses were also conducted on each of the three plant treatments separately using a three-way ANOVA and considering all possible interactions. Impacts on MWD and P dynamics were evaluated using a full factorial model as mentioned above, but with 4 plant treatments included (due to the inclusion of the control microcosms, without plants). For all of the above-mentioned analyses, natural log or Box-Cox power transformations were applied as needed to meet the assumptions of ANOVA (i.e., homoscedasticity and normality). When significant interactions were present between the soil treatments, a Tukey multiple comparisons test was applied to examine all pairwise comparisons between relevant treatment means. All analyses were conducted using JMP Pro 13.0.0 statistical software (SAS_Institute 2016).

3. Results

3.1 Treatment Effectiveness

Overall, microcosms and treatments were effectively maintained throughout the experiment, with 100% plant survival for both *B. decumbens* and *P. vulgaris* up until the time of harvest. Earthworm survival was lower, with only 60% of the added individuals being recovered at the end of the experiment; however, no significant difference in earthworm survival was found between treatments. Additionally, evidence of earthworm activity (e.g., earthworm casts, tunnels, cocoons) was noted at the time of harvest for all microcosms where earthworms were added and in none of the zero earthworm treatments.

3.2 Biomass Production and Nutrient Uptake

When considering microcosms with plants, all soil treatments yielded significant positive impacts on plant growth, with earthworms increasing aboveground and total (root + shoot) biomass by 99% and 91%, respectively, on average across all plant treatments ($p < 0.001$, Table S1). Lime and P fertilizer additions yielded relatively smaller effects, increasing total biomass production by an average of 17% and 13%, respectively, across all treatments ($p < 0.005$). Shoot to root ratio was also influenced by the plant types considered, earthworms and lime, but not by P additions (Table S1). Overall, effects on N content in the plant biomass were similar to those for total biomass, with earthworms increasing average plant N content by 130% across all treatments, compared to an average increase of only 15% with lime and 18% with P additions. While these simple effects on plant growth give an idea about the overall impact of earthworms vs. lime vs. P additions, significant interactions between soil factors (mainly earthworms) and plant treatment (Table S1) led us to focus on separate analyses for each plant treatment.

Microcosms containing only the grass *B. decumbens* responded to all soil factors, and the effects were generally greater than that observed for treatments containing *P. vulgaris*. For example, earthworm presence resulted in a 180% increase for both aboveground and total plant biomass of *B. decumbens* ($p < 0.001$; Table 1), while total biomass increased just 30% with lime ($p = 0.009$) and 22% with P additions ($p = 0.036$). No significant interactions between soil factors were observed (Table 1) for total biomass production in treatments containing only *B. decumbens*. Shoot to root ratio of *B. decumbens* was only influenced by lime additions, such that adding lime on average increased the ratio by 15%. In accordance with the large observed increases in plant biomass, the presence of earthworms yielded a 240% increase in total plant N uptake (root + shoot N) of *B. decumbens*, while no significant N uptake effects were observed for the other soil factors or interaction terms (Table 1). The influence of soil treatments on total P uptake is more complex, with both earthworms and lime (but not P additions) increasing plant P content by roughly 60% ($p < 0.001$); however, there was a significant interaction between lime and P additions ($p = 0.034$; Table 1). Pairwise comparisons based on Tukey tests indicate that P fertilizer increased plant P content in the presence of added lime ($p < 0.001$); but that P in the absence of lime had no effect ($p > 0.10$). Additionally, a significant three-way interaction between earthworms, lime and P addition ($p = 0.033$) suggests that earthworms also play an important role in regulating P uptake by *B. decumbens* (Table 1).

The effect of the different soil factors on the legume, *P. vulgaris*, growing alone was less pronounced than for *B. decumbens*. Earthworms increased aboveground and total biomass by 48% and 35%, respectively ($p < 0.001$), while lime additions increased aboveground biomass production by just 19% ($p = 0.031$) and had no significant effect on total biomass (Table 2). A marginally significant interaction between earthworms and lime ($p = 0.087$) suggests that lime additions increased the biomass of *P. vulgaris* more in the presence of earthworms than in their absence. In addition to their positive effects on overall biomass production, earthworms were found to increase the biomass of plant reproductive parts (beans pods + flowers, a proxy for yield) by 92% ($p = 0.004$; data not shown), while neither lime nor P additions significantly influenced the production of bean pods and flowers. Both earthworms and lime were observed to increase the shoot to root ratio of *P. vulgaris*, by 47% and 32%, respectively ($p < 0.01$). Effects on total plant N content (via soil uptake and fixation) were similar to those observed for biomass. Earthworms were found to increase total plant N content by more than 70% ($p < 0.001$); however, there was a significant interaction between earthworms and lime ($p < 0.001$; Table 2) Pairwise comparisons suggest that this effect was greatly enhanced in the presence of lime ($p < 0.001$), but that lime alone has no effect of total N content of *P. vulgaris* ($p > 0.10$; Fig. 1). While lime additions significantly increased P uptake by *P. vulgaris* overall ($p = 0.007$), there were also significant interactions of lime with both earthworms and P additions ($p < 0.002$; Table 2). Pairwise comparisons indicated that the lime was only effective at increasing P uptake in the presence of earthworms or P fertilizer ($p < 0.001$), but not in their absence ($p > 0.10$).

The combined treatment, with both *B. decumbens* and *P. vulgaris*, yielded intermediate results (relative to the two monocultures) for plant growth and nutrient content. Earthworms increased both aboveground and total biomass production by 89% and 83%, respectively ($p < 0.001$; Table 3). Additions of P fertilizer increased biomass production (aboveground and total) by approximately 30% ($p < 0.001$), while lime had no effect. Shoot to root ratio for the combined treatment was not affected by the soil factors, except for an interaction between earthworms and P additions. As observed for the *P. vulgaris* alone treatment, earthworms more than tripled the biomass of plant reproductive components ($p = 0.003$, data not shown), while lime and P additions had no effect. Earthworms more than doubled N content of the grass-bean mixture ($p < 0.001$), while P additions yielded a 30% increase in N content ($p = 0.025$; Table 3). There were no significant interactions observed between soil factors for biomass production or total biomass N content. Total plant P uptake was increased by lime and P additions by roughly 30% for each ($p < 0.006$), while earthworms yielded only a 20% increase ($p = 0.037$). However, there was a significant interaction between lime and earthworms ($p = 0.004$, Table 3). Tukey tests indicate that lime only increased plant P content in the presence of earthworms ($p < 0.001$), but not in their absence ($p > 0.10$).

3.3 Impacts on Soil Properties

Significant treatment effects were observed for soil structure, such that both earthworms and plant treatments greatly impacted aggregate stability. On average, *B. decumbens* increased MWD by the greatest amount (45% increase relative to the no plant control), while *P. vulgaris* had a lesser effect (20% increase relative to control, Fig. 2). Earthworms also increased MWD by 32% on average ($p < 0.001$); however, a significant earthworm by plant treatment interaction ($p = 0.010$; Fig. 2) indicates the need to consider the effect of earthworms on a treatment-by-treatment basis. In doing so, *P. vulgaris* had virtually no impact on aggregation in the absence of worms (pairwise comparison $p > 0.10$), but MWD increased by 64% when earthworms were present in this treatment ($p < 0.001$). In contrast, *B. decumbens* alone improved aggregation by 36% in the absence of earthworms ($p = 0.058$), whereas earthworms in this plant treatment did not yield significant additional benefits for aggregation ($p > 0.10$). While earthworms can have notable impacts on aggregation in the presence of plants (depending on plant type), they appear to demonstrate virtually no effect on aggregation in microcosms where plants are absent ($p > 0.10$; Fig. 2).

Treatment effects on soil P availability were minimal, with P addition being the only factor that significantly increased resin P at harvest (from 0.33 to 0.94 μg g^{-1}; $p < 0.001$). No significant impacts of earthworms, lime or P additions were observed for soil microbial P (Table S1).

4. Discussion

Findings from this study and previous work in the Llanos suggest that reduced soil biological activity (i.e., macrofauna) associated with intensive management practices (e.g., excessive tillage, agrochemical inputs; see Lavelle et al. 2014) could have important implications for long-term agricultural productivity in the region and needs to be considered in future farm management strategies.

4.1 Relative Impact of Earthworms vs. Soil Fertility Amendments

Earthworms greatly enhanced plant growth in this study, which largely corroborates past results demonstrating the positive effects of earthworms on crop and forage production. In a meta-analyses, van Groenigen *et al.* (2014) reported earthworms to increase the biomass production of grasses by around 25% on average and legumes by only about 10%. With a 180% increase for *B. decumbens* and a 35% increase for *P. vulgaris* (Tables 1 and 2), our study indicates the potential for substantially greater benefits of earthworms to agricultural productivity. Despite the considerably larger biomass increase, our findings broadly fit with those of van Groenigen *et al.* (2014), who report the greatest earthworm benefits in acid soils (pH < 5.6), tropical climates, and for experiments with relatively low N addition (< 30 kg/ ha^{-1}), all conditions that apply to this study. Similarly, Noguera et al. (2010), working with a soil collected from a nearby site in the Llanos region, found *P. corethrurus* to more than double the biomass production of rice in the absence of mineral fertilizer (NPK) inputs. However, relative impacts of earthworms were considerably reduced in a more productive, volcanic ash soil (from the Cauca Dept., Colombia) or with mineral fertilizer additions (Noguera et al. 2010). In another study, Fonte et al. (2012) found similar densities of *P. corethrurus* to increase the biomass production of *B. decumbens* by roughly 30% in a relatively fertile Mollisol. These findings suggest that overall soil fertility and/or nutrient availability likely determines the relative impact of earthworms on productivity across agricultural sites. We note this observation to be of particular relevance for the Llanos and other tropical regions where soils are generally acidic and fertilizer inputs may often be less than optimal (due to local economic constraints), and therefore, earthworms (and associated biological activity) are likely to contribute relatively more to agroecosystem productivity.

Interestingly, we note that the relative effect of earthworms on plant growth was much greater than that of typical application rates of lime and/or P fertilizer, both inputs that are frequently applied in Oxisols globally to manage low pH and associated P limitation. This was especially true in the *B. decumbens* treatments, where earthworms nearly tripled total biomass production compared to increases of less than 30% with lime and P additions (Table 1). While the differences were smaller, earthworms also exhibited greater influence on the growth of *P. vulgaris* than either lime or P additions. Findings by Laossi et al. (2010), working in soils from France, showed a similar result, where the earthworm *Lumbricus terrestris* yielded a comparable effect to mineral fertilizers (48 kg N, 32 kg P and 6.7 kg K ha^{-1}) for both the grass, *Poa annua*, and the legume, *Trifolium dubium*. One key difference in our experiment was the absence of N application, which could have been more limiting to growth than available soil P, and thus reduced the efficacy of lime and P fertilizer alone. However, given that *P. vulgaris* is not likely to be as limited by N, since it has access to biologically fixed N, we suspect that the greater observed benefits of earthworms over P and/or lime additions was not dependent on N limitation. Additionally, we note that higher rates of P fertilizer and lime would likely have produced a larger effect on plant growth, but feel that the levels tested here are representative of many farms in the region and thus are relevant. It is also worth noting that earthworm mortality can provide a significant source of N and P and may have been a factor in microcosms where earthworms died. However, given that we observed significant tunneling and casting activity in all earthworm microcosms and did not observe any correlations between plant growth (or nutrient uptake) and earthworm survival in the microcosms, we feel fairly confident that earthworm effects reported are due mainly to the activity of live earthworms.

4.2 Earthworms Enhance the Efficacy of Common Soil Amendments

While the relatively large impacts of earthworms on plant growth discussed above are indeed important, the interactions observed between earthworms and the fertility amendments are perhaps of greater relevance. For example, in microcosms containing *P. vulgaris*, lime alone, or in combination with P, yielded virtually no increase in biomass production or nutrient uptake relative to the control. However, when lime was added in the presence of earthworms, N uptake was more than doubled (Fig. 1). While not as dramatic, similar effects were also observed for total biomass production and P uptake by *P. vulgaris* (Table 2). These results indicate that earthworms can enhance the efficacy of some soil fertility amendments, and that farmers may be able to improve resource use efficiency by fostering healthy earthworm communities through improved management practices.

A number of mechanisms may be responsible for the observed interactions between earthworms and lime. Given that this effect was only significant for N and P uptake in treatments with the legume, *P. vulgaris*, it may be that earthworms and lime helped to stimulate N availability and/or indirectly enhanced biological N fixation. Earthworms have been shown to enhance the colonization of *Rhizobium* and nodule formation in clover (Doube et al. 1994). Additionally, both earthworms and lime are known to influence soil P availability (Lopez-Hernandez et al. 1993, Fageria and Baligar 2008), which can be an important determinant of N_2 fixation (Snapp et al. 1998, Reed et al. 2007) and overall crop performance, especially in acid soils, like those studied here. Interestingly, we note that neither resin P nor microbial biomass P in the bulk soil increased with lime or earthworms. In a study examining the influence of earthworms on the incorporation of lime in soils, Chan et al. (2003) found pH to increase substantially in earthworm casts, but to show relatively little change in bulk soil. Therefore, we suspect that earthworms may be interacting with lime to increase P availability at a microsite scale (i.e., within soil aggregates formed from their cast; Jimenez et al. 2003), but this effect is not detectable in bulk soil, at least using the P evaluation methods employed here. At the same time, the greater N uptake by *P. vulgaris* in the presence of earthworms and lime may also be associated with increased N availability, as both earthworms and elevated pH can stimulate N mineralization in soils (Curtin et al. 1998, Lubbers et al. 2011).

4.3 Treatment Impacts on Soil Properties

In addition to marked impacts on plant growth and nutrient uptake, the treatments tested in this study provide valuable information on potential belowground impacts of management. Most notably, we observed that both earthworms and plant cover have a positive effect on soil aggregate stability (Fig. 2). More importantly, we observed a significant interaction between the plant and earthworm, such that earthworms had a relatively larger impact in the presence of a legume, *P. vulgaris*, and no effect in the microcosms without plants. This result mirrors findings of previous studies suggesting that earthworms do not contribute to soil structure in the absence of plants or associated organic residues (Fonte and Six 2010, Fonte et al. 2012), since organic matter serves as a food source to stimulate earthworm (and microbial) activity and eventually forms the 'glue' which helps bind soil particles together within earthworm casts to form stable soil aggregates (Blanchart et al. 2004). The greater impact of earthworms in the presence of *P. vulgaris* is likely due to the reduced ability of their roots to aggregate soils, since they are much less fibrous than those of *B. decumbens*. Moreover, earthworm activity is stimulated in the presence of higher residue quality (i.e., higher N concentration that is commonly associated with legumes). Similarly, Velasquez et al. (2012) found the presence of the legume *Arachis pintoi* to stimulate earthworm populations in Brazilian pasture systems and this translated into a greater presence of biogenic (i.e., earthworm derived) aggregates. Improvements to soil structure associated with earthworms and growing plants could have important benefits for water capture, erosion control, gas exchange, root penetration and C stabilization in soils. Our findings highlight the importance of managing vegetative cover in agroecosystems to ensure continuity of plant residue inputs (above and belowground) and protecting soil macrofauna communities. This is especially pertinent for soils in the Llanos which are known to be highly susceptible to compaction and overall degradation of soil structure (Amezquita et al. 2004).

5. Conclusions

With substantial investment from farmers and researchers, the Colombian Llanos is undergoing a rapid transformation to more intensive agriculture, yet the long-term sustainability of this change is not entirely clear. Our findings support previous studies and demonstrate that the common earthworm, *P. corethrurus*, can dramatically increase plant productivity relative to common soil fertility amendments in relatively poor soils from the Llanos. Additionally, earthworms appeared to enhance the efficacy of lime in supporting N uptake (and/or N_2 fixation) in the legume *P. vulgaris*. These results suggest that earthworms and other soil biota can make important contributions to agroecosystem productivity and long-term sustainability in the Llanos This finding highlights the need for developing farming practices and policies that better take into consideration soil biological communities for supporting agricultural productivity, resource use efficiency, and a range of soil-based ecosystem services.

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Table 1: Biomass production and nutrient uptake by the grass *B. decumbens* with and without additions of earthworms (*P. corethrurus*), lime and/or phosphorus to experimental microcosms with soil from the Meta region of Colombia. Values to the right of each mean, in italics, represent the standard error of the mean. ANOVA results for each soil factor and all possible interactions are presented below, with significant effects ($p < 0.05$) in bold. Means and SEs are presented for raw data, while p-values are presented for transformed data.

Worm	**Lime**	**Phosphorus**	**Total Biomass**[a] **(g microcosm^{-1})**	**Shoot:Root Ratio**	**Total Biomass N**[a] **(mg microcosm^{-1})**	**Total Biomass P**[a] **(mg microcosm^{-1})**
Yes	Yes	Yes	2.40 *0.50*	1.96 *0.21*	9.44 *1.56*	1.01 *0.15*
Yes	Yes	No	1.64 *0.18*	1.98 *0.13*	8.88 *0.44*	0.95 *0.14*
Yes	No	Yes	1.95 *0.32*	1.80 *0.08*	10.25 *1.33*	0.56 *0.09*
Yes	No	No	1.38 *0.03*	1.68 *0.11*	8.17 *0.35*	0.51 *0.02*
No	Yes	Yes	0.74 *0.01*	2.02 *0.11*	3.20 *0.01*	0.69 *0.04*
No	Yes	No	0.78 *0.13*	1.86 *0.08*	3.37 *0.66*	0.45 *0.07*
No	No	Yes	0.58 *0.07*	1.63 *0.03*	2.76 *1.00*	0.29 *0.06*
No	No	No	0.49 *0.02*	1.67 *0.04*	2.05 *0.30*	0.47 *0.06*
ANOVA results[b]			**p-value**	**p-value**	**p-value**	**p-value**
Earthworm			**< 0.001**	0.439	**< 0.001**	**< 0.001**
Lime			**0.009**	**0.004**	0.151	**< 0.001**
Phosphorus			**0.036**	0.520	0.426	0.891
Earthworm x Lime			0.356	0.684	0.144	0.438
Earthworm x Phosphorus			0.143	0.996	0.870	0.648
Lime x Phosphorus			0.690	0.918	0.478	**0.034**
Earthworm x Lime x Phosphorus			0.563	0.252	0.965	**0.033**

[a] includes above- and belowground biomass

[b] p-values represent ln transformed data for all variables

Table 2: Biomass production and nutrient uptake by the legume *P. vulgaris* with additions of earthworms (*P. corethrurus*), lime and/or phosphorus to experimental microcosms with soil from the Meta region of Colombia. Values to the right of each mean, in italics, represent the standard error of the mean. ANOVA results for each soil factor and all possible interactions are presented below, with significant effects ($p < 0.05$) in bold. Means and SEs are presented for raw data, while p-values are presented for transformed data.

Worm	**Lime**	**Phosphorus**	**Total Biomass**[a] (**g microcosm**$^{-1}$)		**Shoot:Root Ratio**		**Total Biomass N**[a] (**mg microcosm**$^{-1}$)		**Total Biomass P**[a] (**mg microcosm**$^{-1}$)	
Yes	Yes	Yes	2.05	*0.26*	4.81	*0.68*	43.35	*13.10*	3.31	*0.51*
Yes	Yes	No	2.30	*0.24*	4.59	*0.55*	20.86	*2.29*	2.07	*0.29*
Yes	No	Yes	1.73	*0.01*	3.18	*0.50*	17.08	*2.40*	1.24	*0.15*
Yes	No	No	1.70	*0.06*	3.20	*0.35*	18.12	*2.63*	1.40	*0.06*
No	Yes	Yes	1.31	*0.13*	2.52	*0.39*	12.90	*0.42*	2.04	*0.07*
No	Yes	No	1.56	*0.13*	3.23	*0.26*	12.42	*0.56*	1.47	*0.19*
No	No	Yes	1.35	*0.06*	2.54	*0.20*	12.70	*0.64*	1.92	*0.08*
No	No	No	1.51	*0.16*	2.27	*0.24*	14.04	*1.51*	2.39	*0.23*
ANOVA results[b]			**p-value**		**p-value**		**p-value**		**p-value**	
Earthworm			**< 0.001**		**0.001**		**< 0.001**		0.557	
Lime			0.086		**0.009**		0.171		**0.007**	
Phosphorus			0.133		0.721		0.692		0.137	
Earthworm x Lime			0.087		0.242		**0.033**		**< 0.001**	
Earthworm x Phosphorus			0.475		0.646		0.449		0.494	
Lime x Phosphorus			0.396		0.393		0.123		**0.001**	
Earthworm x Lime x Phosphorus			0.779		0.246		0.790		0.884	

[a] includes above- and belowground biomass

[b] p-values represent ln transformed data for all variables except Total Biomass N where a Box-Cox transformation was used

Table 3: Biomass production and nutrient uptake by the species mixture of *B. decumbens* and *P. vulgaris* with additions of earthworms (*P. corethrurus*), lime and/or phosphorus to experimental microcosms with soil from the Meta region of Colombia. Values to the right of each mean, in italics, represent the standard error of the mean. ANOVA results for each soil factor and all possible interactions are presented below, with significant effects ($p < 0.05$) in bold. Means and SEs are presented for raw data, while P-values are presented for transformed data.

Worm	**Lime**	**Phosphorus**	**Total Biomass**[a] **(g microcosm^{-1})**		**Shoot:Root Ratio**		**Total Biomass N**[a] **(mg microcosm^{-1})**		**Total Biomass P**[a] **(mg microcosm^{-1})**	
Yes	Yes	Yes	2.65	*0.15*	2.35	*0.49*	18.19	*2.37*	1.93	*0.08*
Yes	Yes	No	1.75	*0.14*	3.02	*0.26*	12.75	*0.77*	1.30	*0.02*
Yes	No	Yes	2.17	*0.31*	2.05	*0.13*	21.97	*3.33*	1.16	*0.16*
Yes	No	No	1.57	*0.07*	2.36	*0.16*	13.99	*1.63*	0.78	*0.02*
No	Yes	Yes	1.21	*0.18*	2.64	*0.10*	10.29	*3.40*	1.31	*0.30*
No	Yes	No	1.04	*0.06*	1.93	*0.23*	7.44	*0.40*	0.83	*0.07*
No	No	Yes	1.17	*0.06*	2.15	*0.22*	7.33	*0.26*	0.98	*0.03*
No	No	No	0.95	*0.03*	2.03	*0.13*	7.00	*0.51*	1.09	*0.15*
ANOVA results[b]			**P-value**		**P-value**		**P-value**		**P-value**	
Earthworm			**< 0.001**		0.189		**< 0.001**		**0.037**	
Lime			0.110		0.113		0.955		**0.006**	
Phosphorus			**0.001**		0.860		**0.025**		**0.004**	
Earthworm x Lime			0.396		0.543		0.210		**0.004**	
Earthworm x Phosphorus			0.147		**0.015**		0.238		0.183	
Lime x Phosphorus			0.867		0.664		0.876		0.132	
Earthworm x Lime x Phosphorus			0.487		0.179		0.544		0.157	

[a] includes above- and belowground biomass

[b] P-values represent ln transformed data for all variables

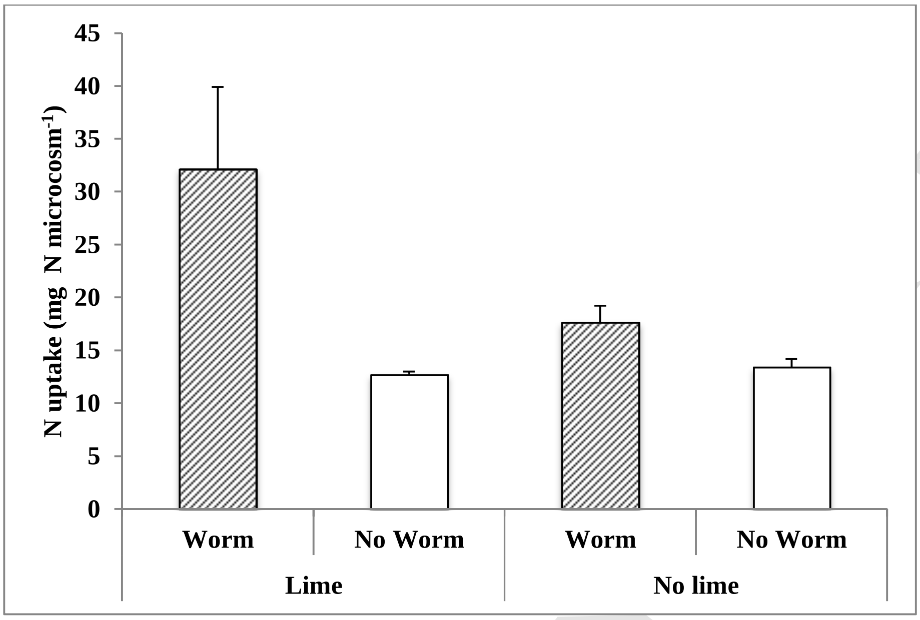

Figure 1: Mean N content (shoots and roots) of *P. vulgaris* plants grown in microcosms with and without earthworms (*P. corethrurus*) and/or lime additions in soil from the Meta region of Colombia. Error bars represent the standard error of the mean.

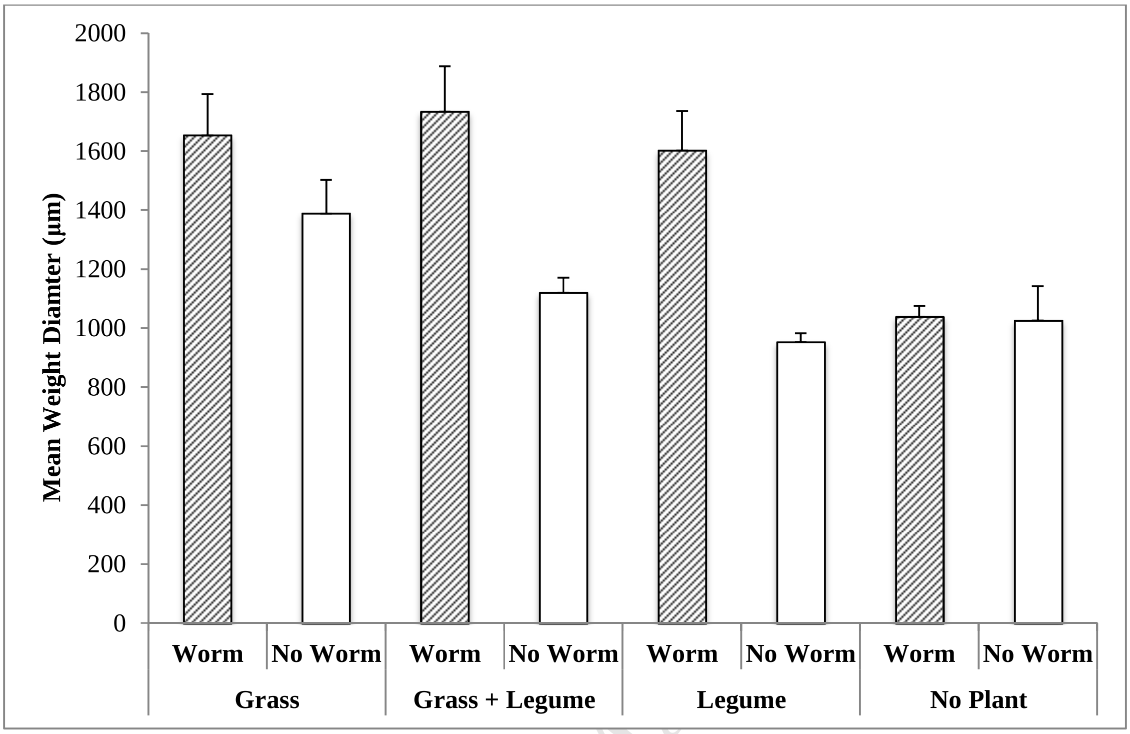

Figure 2: Aggregate stability (Mean Weight Diameter) of soils from the Meta region of Colombia in microcosms under different four plant treatments (1. the grass *B. decumbens* alone, 2. the legume *P. vulgaris* alone, 3. combination of the two species, or 4. no plants) and two earthworm treatments (with and without *P. corethrurus*) in all possible combinations. Error bars represent the standard error of the mean.

Table S1: P-values for ANOVA examining the impacts of plant treatments (*B. decumbens* alone, *P. vulgaris* alone, and the combination of the two species), earthworms (*P. coretherus*), lime and phosphorus (each factor alone and in all possible combinations) on key plant growth and soil parameters in experimental microcosms with soil from the Meta region of Colombia. Values to the right of each mean, in italics, represent the standard error of the mean. All variables were ln transformed to meet the assumptions of ANOVA. All significant effects ($P < 0.05$) are presented in bold font. Means and SEs are presented for raw data, while P-values are presented for transformed data.

Experimental Factor/s Considered	**Total Biomass**[a] **(g microcosm^{-1})**	**Shoot:Root Ratio**	**Total Biomass N**[a] **(mg microcosm^{-1})**	**Total Biomass P**[a] **(mg microcosm^{-1})**	**Aggregate Stability (MWD µm)**	**Available Soil P (µg g soil^{-1})**	**Microbial P in Soil (µg g soil^{-1})**
Plant	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**	0.990	0.732
Earthworm	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**	0.157	0.479
Lime	< **0.001**	< **0.001**	**0.037**	< **0.001**	0.463	0.285	0.879
Phosphorus	**0.004**	0.877	**0.015**	**0.010**	0.724	< **0.001**	0.375
Plant x Earthworm	< **0.001**	**0.003**	**0.000**	**0.001**	**0.010**	0.447	0.258
Plant x Lime	0.240	0.271	0.350	**0.043**	0.255	0.838	0.593
Plant x Phosphorus	**0.002**	0.834	0.579	0.114	0.807	0.349	0.970
Earthworm x Lime	0.507	0.267	0.757	< **0.001**	0.982	0.365	0.594
Earthworm x Phosphorus	**0.031**	0.211	0.122	0.166	0.132	0.240	0.779
Lime x Phosphorus	0.531	0.727	0.508	< **0.001**	0.643	0.051	0.946
Plant x Earthworm x Lime	0.153	0.456	**0.010**	**0.018**	0.448	0.296	0.096
Plant x Earthworm x Phosphorus	0.671	**0.047**	0.667	0.845	0.806	0.099	0.559
Plant x Lime x Phosphorus	0.809	0.516	0.180	0.410	0.326	0.633	0.285
Earthworm x Lime x Phosphorus	0.526	0.738	0.681	**0.024**	0.354	0.943	0.899
Plant x Earthworm x Lime x Phosphorus	0.755	0.103	0.431	0.130	0.610	0.572	0.386

[a] includes above- and belowground biomass

Title: Earthworms regulate productivity and efficacy of soil fertility amendments in acid soils of the Colombian Llanos

Highlights:

- Earthworms enhance plant growth more than lime or P fertilizer
- Lime only improves plant N uptake in the presence of earthworms
- Earthworms enhance soil structure, but only in the presence of growing plants
- Farm management should consider soil biological communities to optimize resource use efficiency