RESEARCH ARTICLE

Influence of scattered trees in grazing areas on soil properties in the Piedmont region of the Colombian Amazon

Faver Álvarez¹,²,³, Fernando Casanoves⁴, Juan Carlos Suárez⁵,⁶,⁷ *

¹ Programa de Medicina Veterinaria y Zootecnia, Facultad de Ciencias Agropecuarias, Universidad de la Amazonia, Florencia, Caquetá, Colombia, ² Laboratorio de Evaluación de Forraje y Nutrición Animal, Centro de Investigaciones Amazónicas CIMAZ Macagual, Universidad de la Amazonia, Florencia, Caquetá, Colombia, ³ Grupo de Investigación en Sistemas Agroforestales para la Amazonia -GISAPA, Universidad de la Amazonia, Florencia, Caquetá, Colombia, ⁴ CATIE-Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica, ⁵ Maestría Sistemas Sostenibles de Producción, Facultad de Ciencias Agropecuarias, Universidad de la Amazonia, Florencia, Caquetá, Colombia, ⁶ Centro de Investigaciones Amazónicas CIMAZ Macagual, Grupo de Investigaciones Agroecosistemas y Conservación en Bosques Amazónicos-GAIA, Florencia, Caquetá, Colombia, ⁷ Programa de Ingeniería Agroecológica, Facultad de Ingeniería, Universidad de la Amazonia, Florencia, Caquetá, Colombia

* juansuarez1@gmail.com

Abstract

Trees dispersed in grazing areas are contribute to the sustainability of livestock systems. The interactions between trees and soil are ecological processes that allow the modification of the biology, fertility, and physics of the soil. This study was aimed to assess the influence of dispersed trees in pastures on soil properties in grazing areas for dual-purpose cattle systems in the Piedmont region of the Colombian Amazon. The work was done in grazing areas with scattered trees at the Centro de Investigaciones Amazónicas CIMAZ–Macagual in Florencia—Caquetá—Colombia. We evaluated the effect of five tree species, Andira inermis, Bellucia pentámera, Guarea Guidonia, Psidium guajava and Zygia longifolia, on soil properties (up to 30 cm soil depth) under and outside the influence of the crown. Under the tree crown, three points were systematically taken in different cardinal positions. This was done at a distance corresponding to half the radius of the tree crown. The sampling points in the open pasture area (out of crown) were made in the same way, but at 15 m from the crown border. The ANOVA showed significant interaction (P < 0.0001) between tree species and location for macrofauna abundance up to 30 cm soil depth. For this reason, we performed the comparison between locations for each tree species. Chemical soil variables up to 10 cm soil depth only showed interaction of tree species-location for exchangeable potassium (P = 0.0004). Soil physical soil characteristics up to 30 cm soil depth only showed interaction of tree species-location at 20 cm soil depth (P = 0.0003). The principal component analysis for soil properties explained 61.1% of the total variability of the data with the two first axes. Using Monte Carlo test, we found crown effect for all species. Trees help to control exchangeable mineral elements that can affect the soil, potentiate basic cations such as magnesium and potassium, increase the abundance of soil macrofauna; but some trees with high ground level of shade in grazing areas could increase soil compaction due to the greater concentration of cattle in these areas.
Introduction

The department of Caquetá is located in the northwest of the Amazon region. It has an area of 89,530 km² that corresponds to 7.8% of the country’s continental surface; it is part of the so-called Western Amazon subregion of Colombia [1]. In this region, livestock activity occurs in all types of farm landscapes, whose sizes vary from 30 ha to more than 500 ha, with an average of 120 bovines per farm [2]. Historically, there were changes in land use cover that started from the forest to agricultural production systems (annual crops, palm, and pastures) which were sponsored by state policies. This process has been called by some authors as the empowerment of the Amazon, causing the loss of ecosystem services, as well as reduced livestock systems efficiency [3].

In this context, deforestation and the conversion of Amazonian forests into pastures and croplands can have negative effects on the soil due to an excessive stocking, turning grazing areas into degraded pastures [4]. This practice has increased compaction, erosion, nutrient depletion, and general loss of soil fertility and biodiversity [5–8]. The soil macrofauna in particular has proven to be a sensitive indicator of the alteration of the vegetation cover [8–12], and it can considerably affect the decomposition and cycling processes of soil nutrients [13–15].

The conservation of the tree component in grazing areas allows transforming traditional livestock systems into more sustainable productive systems [3]. In addition, it is important to know the effect of scattered trees in pastures on soil properties [16, 17], ecosystem services [18] and animal production [19, 20]. The presence of trees in pastures have several agroecological advantages [21]. These include a higher content of soil nutrients, although well below that of the amount stored in the natural forest [22] and the growth of tree seedlings and crop species under its crown [23]. Likewise, the distribution and nature of plants in an agroforestry system greatly influence soil biology [24–26]. The particular trophic and microclimatic conditions in the vicinity of the trees can affect the abundance and richness of soil macrofauna [27].

Scattered trees in paddocks contribute to improve soil fertility [28], but the level of improvement depends on the tree species and functional traits such as leaf type and size, crown size, and architecture, among others [29], their arrangement and spatial distribution, and the management given to the scattered trees [30, 31]. Knowing the impact of scattered trees in pastures on soil characteristics (biological, chemical, and physical) will contribute to better pasture management decisions including animal stocking rate applied. This is, because pasture and tree biomass production depends on changes in soil fertility [32]. The objective of this work was to determine the effect of the most common tree species scattered in pastures on the biological, chemical, and physical properties of the soils in grazing areas of managed dual-purpose cattle systems in the Piedmont region of the Colombian Amazon. We expect to find a significant effect of tree canopy on soil variables, with the effect of some tree species on biological, chemical, and physical variables being more significant. We tested the two specific hypothesis: i) tree canopy has a significant effect on soil variables, and ii) tree species common of cattle farms in the Colombian Amazon region influence soil properties.

Materials and methods

Study area

The study was carried out at the Centro de Investigaciones Amazónicas CIMAZ–Macagual "Cesar Augusto Estrada González", located 22 km from Florencia, a city in the south of the Caquetá department—Colombia, with about 380 ha for livestock production. It is geographically located in the Colombian Amazon at 1° 37’ N and 75° 36’ W, at 300 m above sea level,
and Afm type (Warm-Humid Tropical Forest) in the climatic classification according to Köppen [33]. The area presents average annual precipitation of 3,793 mm, a solar brightness of 1,707 h year−1, an average temperature of 25.5˚C and relative humidity of 84.25%. It is located within the life zone of the Tropical Humid Forest (Bh-T) defined by Holdridge [34].

Tree selection and sampling points

Five tree species Andira inermis, Bellucia pentámera, Guarea Guidonia, Psidium guajava and Zygia longifolia were selected to evaluate the influence of scattered trees on the soil properties in grazing areas of the managed pastures. These species were selected because they were the ones that presented the highest value index of ecosystem importance in a census of 4,657 trees in the cattle farms in the Colombian Amazon region [35]. Except for Guarea guidonia, they were the most named by the cattle producers of the region in a study on local knowledge and provision of ecosystem services [35]. Two individuals of each tree species that did not have overlapping crowns and shade areas to ensure the independence of the observations were randomly selected within the paddocks as replications. Individuals within a tree species were similar in architecture, shape, height, and crown size. In each individual tree, three sampling points were taken in the North, East and West position in the middle of the radius of the crown (distance below the crown). The sampling points in the open pasture area (outside of crown) were carried out in a North, East, and West position, 15 m from the edge of the crown of each individual tree (distance out of crown) selected for soil sampling.

Evaluation of soil biological, chemical, and physical characteristics

We evaluated biological, chemical, and physical characteristics of soils sampled under and outside tree effect in all sampling points. For the characterization of the soil macrofauna, we used the ISO 23611–5 standard [36]. A soil monolith was taken (25 × 25 cm at a soil depth of 30 cm) and for the extraction of this monolith we used a metallic angle frame. For each tree and distance to the crown of the tree (below or outside), all the fauna of the soil in the young and adult stage found in the litter, and in the 30 cm of soil was taken without differentiating by depth, for a total of 60 data (5 species × 2 repetitions × 2 distances to the crown of the tree × 3 positions). The collected fauna samples were placed in plastic bottles with 97% alcohol, and later a morphological description and a taxonomic classification were made at the order level of the individuals found.

For chemical characterization of the soil, a composed sample of three cardinal positions at 0–10 cm depth was taken for each tree and distance to the crown of the tree (below or outside) obtaining 180 observations (5 species × 2 repetitions × 2 distances to the crown of the tree × 3 positions × 3-fold soil lab determinations). The three lab determinations were averaged to yield n = 60 data points. For each soil sample we determined: i. soil organic carbon (SOC) by oxidation of dichromate [37] in an acid medium for 30 min in a digester block at a constant temperature of 155˚C, and titration of the non-oxidized dichromate employing Mohr’s salt; ii. Soil organic matter (SOM) was estimated by multiplying the SOC value with 1.7 [38]; iii. exchangeable cations (Ca²⁺, Na⁺, Mg²⁺, K⁺) and exchangeable aluminum (Al³⁺) extracted by successive washes with a 0.2 N BaCl solution in an extract-soil ratio of 1:5 following the method of Mehlich [39] with the modification highlighted by Lax et al. [40]. The concentrations of the exchangeable cations and Al were determined by Ion Chromatography (IC) in an accredited laboratory; iv. estimation of aluminum saturation (AlS); v. available inorganic phosphorus (P) extracted by the Olsen method [41] using bicarbonate (0.5M NaHCO₃) at pH 8.5, in a solution-soil ratio of 1:20 [42]. The phosphorus resulting from the extracts, previously neutralized with a dilute HCl solution, was determined calorimetrically by the ascorbic acid
method according to Murphy and Riley [43]; vi. potentiometric hydrogen potential (pH); and vii. cation exchange capacity (CEC).

For characterization of soil physical characteristics, we used a 50 × 50 × 50 cm test pit sampling in the three positions (N, W, E) at 0–10, 10–20, and 20–30 cm depth for each tree and distance to the crown of the tree (below or outside), obtaining 60 observations (5 species × 2 repetitions × 2 distances to the crown of the tree × 3 positions) for each of the three depths. Using the volume cylinder method [44] (98.1 cm$^3$) the percentage of moisture and the bulk density of soil were determined. Likewise, the soil resistance to penetration was determined using a hand penetrometer model 0601 (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands).

Data were analyzed through an analysis of variance with linear mixed models (LMM) for continuous variables and generalized linear mixed models (GLMM) with a Poisson distribution for the abundance and richness of macrofauna orders. The model considered the fixed effects of the tree species, distance to the crown of the tree (below or outside), and the interaction species by distance to the crown, and the random effects of tree [45] and position within tree. To determine differences between treatment means, Fisher’s LSD test was used (p < 0.05) and in cases where there were interactions between species and distance factors, orthogonal contrasts were used to determine differences between distance within each species. The analysis was performed using the InfoStat program [46] and its interface to R [47].

Principal component analysis (PCA) was carried out to explore the relationship between biological variables, and between chemical and physical variables and to determine multivariate differences between tree species and association among variables. Significance was tested using a Monte Carlo test (1,000 simulations). PCA allows to analyze the interdependence of metric variables and to find an optimal graphical representation of the variability of the data in a table of n observations and p columns or variables. This exploratory analysis tries to find, with minimal loss of information, a new set of uncorrelated variables (principal components) that explain the structure of variation in the rows of the data table. Additionally, co-inertia analysis was used to explore covariation and general similarity in data structure between the soil biological, chemical, and physical data sets. Multivariate analysis was performed in R.3.4.4 software [47], using the Ade4 package.

Results
Soil biological characteristics

The analysis of variance using a GLMM showed highly significant differences (P < 0.0001) for the abundance of macroinvertebrate orders between distance to the crown of the tree (below or outside) (29.26 ± 2.22 and 22.66 ± 1.77 below and outside of crown, respectively, Fig 1). However, the model showed significance in the interaction of tree species by distance (P = 0.0004), for which the positions within each tree species were compared. Guarea guidonia and Zygia longifolia presented higher abundance below the crown (40.14 ± 6.62 for Z. longifolia and 23.04 ± 4.01 for G. guidonia) than outside the crown (25.38 ± 4.36 for Z. longifolia and 14.97 ± 2.76 for G. guidonia) (Fig 1). Andira inermis, Psidium guajava, and Bellucia pentamera did not show differences between locations.

For the variable on richness of macroinvertebrate orders, there was no interaction between tree species and distance (P = 0.5831), and there were no differences between the two distances (P = 0.6557). But there were differences between tree species (P = 0.0378), where A. inermis was the one with the highest richness (4.82 ± 0.63), followed by Z. longifolia (4.52 ± 0.62), B. pentamera (4.14 ± 0.59), P. guajava (2.91 ± 0.49), and ending with G. Guidonia (2.74 ± 0.48) (Table 1).
Fig 1. Abundance of macroinvertebrates below and outside the crown of tree species in grazing areas of pastures in the Colombian Amazonian piedmont. Equal letters within a species indicate equal means (P > 0.05).

https://doi.org/10.1371/journal.pone.0261612.g001

Table 1. Macroinvertebrate richness in scattered trees in grazing areas of pastures in the Colombian Amazonian piedmont.

| Tree species       | Mean  | S.E.     | p-value |
|--------------------|-------|----------|---------|
| Andira inermis     | 4.82  | 0.63a    | 0.0378  |
| Bellucia pentamera | 4.14  | 0.59ab   |         |
| Guarea guidonia    | 2.74  | 0.48b    |         |
| Psidium guajava    | 2.91  | 0.49b    |         |
| Zygia longifolia   | 4.52  | 0.62a    |         |

Equal letters between species indicate equal means (P > 0.05).

https://doi.org/10.1371/journal.pone.0261612.t001
Soil chemical characteristics

For the chemical characteristics evaluated, the analysis under the LMM only showed significant interaction ($P = 0.0046$) between tree species and distance for the $K^+$ variable. Differences were found between below and outside of crown ($P = 0.0410$), with the highest average content of $K^+$ under the crowns ($0.71 \pm 0.06 \text{ cmol kg}^{-1}$) than outside these ($0.54 \pm 0.06 \text{ cmol kg}^{-1}$). *Psidium guajava* and *Z. longifolia* presented higher $K^+$ content below the crown ($1.09 \pm 0.13 \text{ cmol kg}^{-1}$ and $0.80 \pm 0.13 \text{ cmol kg}^{-1}$ respectively) than outside of crown ($0.59 \pm 0.13 \text{ cmol kg}^{-1}$ and $0.31 \pm 0.13 \text{ cmol kg}^{-1}$ respectively) (Fig 2). For *B. pentamera* and *A. inermis*, there were no differences between distance. *Guarea guidonia* presented differences between distance, but here the highest $K^+$ content occurred at the outside of crown distance ($0.81 \pm 0.13 \text{ cmol kg}^{-1}$) and not under the crown distance ($0.31 \pm 0.13 \text{ cmol kg}^{-1}$) (Fig 2).

The rest of the soil chemical variables evaluated did not present significant differences for tree species by distance interaction and the distance effect. Thus, only results on differences between tree species are presented. For soil pH, analysis showed differences ($P = 0.0337$) between species with *A. inermis* and *Z. logifolia* presenting highest mean values ($5.42 \pm 0.14$ and $5.14 \pm 0.14$, respectively) (Table 2). Differences for Al saturation (%) were found between species ($P = 0.0144$) where *B. pentamera* presented the highest percentage with a mean of $71.80 \pm 0.22$ and *Z. logifolia* presented the lowest percentage with a mean of $21.72 \pm 6.46$ (Table 2). For exchangeable Al value differences between species ($P = 0.0050$), *B. pentamera* presented...
presented the highest content with 8.27 ± 0.78 cmol kg⁻¹, and *Z. logifolia* presented the lowest content with 0.90 ± 0.78 cmol kg⁻¹ (Table 2).

The cation exchange capacity (CEC) showed differences between species (*P* = 0.0065), with the highest mean for *B. pentamera* of 25.43 ± 1.29 cmol kg⁻¹, and *A. inermis* with the lowest level with 12.15 ± 1.29 cmol kg⁻¹ (Table 2). Exchangeable sodium values presented differences between species (*P* = 0.0056), where *Z. longifolia* showed the highest mean with 0.16 ± 0.01 cmol kg⁻¹, and *P. guajava* showed the lowest mean with 0.09 ± 0.01 cmol kg⁻¹ (Table 2). Available P content presented significant differences (*P* = 0.0123), where *A. inermis* presented the highest mean with 52.17 ± 5.05 cmol kg⁻¹, and *P. guajava* presented the lowest mean with 11.98 ± 5.05 cmol kg⁻¹ (Table 2). Soil organic carbon (SOC), soil organic matter (SOM), calcium (Ca), and exchangeable magnesium (Mg) did not show differences (*P* < 0.05) between species or distance.

### Soil physical characteristics

The analysis of variance of soil physical variables showed significance only for the interaction distance by tree species for bulk density at 20 cm depth (*P* = 0.0003). At other soil depths, no interaction or effect of distance or species was found. *Psidium guajava* presented higher soil bulk density values outside of crown (1.19 ± 0.03 g cm⁻³) than below its crown (1.13 ± 0.03 g cm⁻³). *A. inermis* presented a higher bulk density under its crown (1.05 ± 0.03 g cm⁻³) than outside of it (0.95 ± 0.03 g cm⁻³). *G. guidonia*, *B. pentamera* and *Z. longifolia* did not show differences in any of the two distances at 20 cm soil depth (Fig 3).

For the variable resistance of the soil to penetration at the three depths evaluated, the interaction between distance by tree species was found (*P* < 0.0001). Greater resistance to the soil penetration was detected under *Z. longifolia* (191.47 ± 16.67 kPa cm⁻²) than outside it at 10 cm (96.25 ± 16.67 kPa cm⁻²), at 20 cm (195.83 ± 17.91 kPa cm⁻² and 106.67 ± 17.91 kPa cm⁻² respectively), and at 30 cm (197.50 ± 17.66 kPa cm⁻² and 106.67 ± 17.66 kPa cm⁻²), respectively. The species *G. guidonia*, *A. inermis*, *P. guajava* y *B. pentamera* did not show significant differences in the two distances at all depths (Table 3).

The variable moisture at ground level at 20 cm depth showed significant (*P* = 0.0073) effects between tree species and distance. Moreover, the species evaluated *A. inermis* presented a lower percentage of moisture below its crown (0.35 ± 0.02) than outside of it (0.44 ± 0.02), while *P. guajaba*, *Z. longifolia*, *G. Guidonia*, and *B. pentàmera* did not show significant differences in any distance (Fig 4).

### Relationships between edaphic properties and tree species

The PCA for the macrofauna groups explained 42.3% of the variability of the data with the first two components. PC₁ projected the incidence of the crown of each species on the

---

**Table 2. Differences between tree species for the soil chemical variables (Mean±S.E.).**

| Tree Species       | CEC (cmol kg⁻¹) | Exchangeable sodium (cmol kg⁻¹) | Available Phosphorus (mg kg⁻¹) | pH       | Exchangeable aluminum (cmol kg⁻¹) | Al saturation (%) |
|--------------------|----------------|-------------------------------|-------------------------------|----------|----------------------------------|-------------------|
| *Andra inermis*    | 12.15±1.29c    | 0.12±0.01b                    | 52.17±5.05a                   | 5.42±0.14a | 0.95±0.07c                       | 30.7±7.14cd       |
| *Bellucia pentamera* | 25.43±1.29a   | 0.11±0.01bc                   | 26.74±5.05b                   | 4.62±0.14b | 8.27±0.78a                       | 71.93±6.46a       |
| *Guarea guidonia*  | 16.78±1.29bc   | 0.09±0.01c                    | 27.88±5.05b                   | 5.01±0.14ab| 1.75±0.82bc                      | 46.21±6.75bc      |
| *Psidium guajava*  | 18.89±1.29b    | 0.09±0.01c                    | 11.98±5.05b                   | 4.55±0.14b | 4.22±0.78bc                      | 58.48±6.46ab      |
| *Zygia longifolia* | 17.4±1.29b     | 0.16±0.01a                    | 46.52±5.05a                   | 5.14±0.14a | 0.9±0.78c                        | 21.72±6.46d       |

Equal letters between species indicate equal means (*P* > 0.05, n = 36). C.E.C: Cation Exchange Capacity.
distribution of macrofauna groups. For instance, the soils below the species *Andira inermis* and *Zygia longifolia* were related to Araneae, Hemiptera, Diptera, and Gasteropoda, while those of *Bellucia pertamera* and *Psidium guajava* were related to the Homoptera and Diplopoda. The PC$_2$ projected the Dermaptera group in the upper part and the Coleoptera group in its lower part. Both groups did not show a strong relationship with any tree species. The separation of the tree species according to the macrofauna groups was significant, indicating the incidence of the species on the macrofauna ($P = 0.0281$) (Fig 5).

The PCA for edaphic properties (physical and chemical) explained 61.2% of the total variability of the data with the first two components. PC$_1$ is related to the species *P. guajava* and *B. pentamera*.

Table 3. Penetration resistance (Mean±S.E.) in the combination of tree species by distance at three different depth in grazing areas of pastures in the Colombian Amazon.

| Tree Species | Soil resistance at 10 cm (kPa cm$^{-2}$) | Soil resistance at 20 cm (kPa cm$^{-2}$) | Soil resistance at 30 cm (kPa cm$^{-2}$) |
|--------------|-----------------------------------------|-----------------------------------------|-----------------------------------------|
|              | Below crown    | Outside of crown | Below crown    | Outside of crown | Below crown    | Outside of crown |
| *Andira inermis* | 171.88±16.67a | 157.02±16.67a | 194.38±17.91a | 186.5±17.91a | 195.27±17.66a | 189.63±17.66a |
| *Bellucia pentamera* | 99.88±16.67a | 92.23±16.67a | 99.88±17.91a | 90.12±17.91a | 90.25±17.66a | 82.27±17.66a |
| *Guarea guidonia* | 181.15±16.67a | 171.13±16.67a | 200.38±17.91a | 193.38±17.91a | 213.4±17.66a | 215.77±17.66a |
| *Psidium guajava* | 111.83±16.67a | 111.42±16.67a | 124.58±17.91a | 112.58±17.91a | 120.17±17.66a | 109.5±17.66a |
| *Zygia longifolia* | 191.47±16.67a | 96.25±16.67b | 195.83±17.91a | 106.67±17.91b | 197.5±17.66a | 106.67±17.66b |

Equal letters between species indicate equal means ($P > 0.05$).
pentamera with the highest Al saturation, moisture, CEC, SOC and SOM; while the species A. inermis and Z. longifolia are characterized by having higher values of pH, soil resistance to penetration, available P, exchangeable Ca, and silt. PC2 separated the species Z. longifolia characterized by having the highest levels of exchangeable Mg and Na. The effect under the cover of the species were significant according to the Monte Carlo test (Fig 6).

When investigating the relationships between data sets of tree species using Co-inertia analysis, eight significant correlations were found. All tree species obtained significant relationships when contrasting the chemical and physical properties of the soil, except for P. guajava. Regardless of the arboreal species, significant relationships were found under the cover when macrofauna data were contrasted with the physical and chemical properties of the soil (Table 4).

**Discussion**

The greater abundance of the macrofauna below the crown of A. inermis, G. guidonia, P. guajava, and Z. longifolia trees than abundance outside of crown in grazing areas of pastures is presumably due to two factors: the quality of litter and microclimatic conditions. Trees that are present in grazing areas contribute to the SOM of soil due to the entry of senescent leaves, bark, branches, and roots to the system that are decomposed by the macrofauna [48]; and the
presence of these individuals depends on the quantity and quality of litter provided by each species [49]. The factor that had the greatest impact on macrofauna populations was the distance, a situation that has also been described for other tree species such as *Croton megalocarpus*, *Eucalyptus grandis* and *Zanthoxylum gilletii* [50]. Likewise, this higher population below the crown is due to traits related to the quality of the leaf litter, which influences the increase of individuals under this position [50].

In our study we found differences in macrofaunal populations according to tree species, a condition that has been a characteristic in different studies. For example, Vohland and Schroth [51] found that the general abundance of fauna was significantly higher in *Bactris gasipaes* and *Bixa orellana* compared to that obtained in *Bertholletia excelsa* and *Theobroma grandiflorum*, because of differences in the quality of plant tissue. Similarly, Gholami et al. [52] found that the abundance and diversity of the macrofauna were spatially related to the density of tree cover, the diversity, and uniformity of the tree species and that they may be related to the

Fig 5. Projection on the factorial plane of the first two axes of a principal component analysis of the edaphic macrofauna variables and of the sampling points grouped according to tree species. A. Correlations of edaphic macrofauna groups. B. Sorting of samples by macrofaunal variables and identified by tree species.

https://doi.org/10.1371/journal.pone.0261612.g005
microclimate conditions provided by them, showing that the density of trees and their diversity could be the key drivers of the spatial pattern of soil macrofauna diversity.

On the other hand, Laossi et al. [53] have pointed out that the abundance of soil fauna is affected by the quality of the litter and to a greater extent by its quantity. *Zygia longifolia* and

Fig 6. Projection on the factorial plane of the first two axes of a principal component analysis of edaphic variables and sampling points grouped according to tree species. A. Macrofauna correlations. B. Sorting of samples by edaphic variables according to tree species.

Table 4. Matrix coefficient (RV) between the three datasets for tree species and location.

| Species             | Macrofauna—soil chemical | Macrofauna—soil physical | Soil chemical—soil physical |
|---------------------|--------------------------|--------------------------|-----------------------------|
|                     | RV                       | p-value                  | RV                          | p-value                  |
| *Andira inermis*    | 0.277                    | 0.433                    | 0.324                       | 0.425                    |
| *Bellucia pentámera*| 0.453                    | 0.076                    | 0.430                       | 0.166                    |
| *Guarea guidonea*   | 0.387                    | 0.599                    | 0.434                       | 0.448                    |
| *Psidium guajava*   | 0.464                    | 0.112                    | 0.285                       | 0.733                    |
| *Zygia longifolia*  | 0.376                    | 0.481                    | 0.428                       | 0.091                    |
| Below crown         | 0.277                    | 0.008*                   | 0.288                       | 0.011*                   |
| Outside of crown    | 0.168                    | 0.418                    | 0.205                       | 0.235                    |
A. inermis presented the highest values in the abundance of the macrofauna under their covers. These two species offer a high level of shade (they have a dense crown), which can probably influence the microclimatic conditions of the soil under their crown. It has been reported in several studies that below the cover of trees under tropical conditions, the temperature is on average 2 to 3°C lower than in open areas [54] and in some sites the difference may reach up to 9.5°C [55], thus affecting air/soil temperature [56, 57] and soil moisture [58, 59]. These conditions are important as many soil organisms are sensitive to soil moisture and temperature regimes [60].

The importance of trees in grazing areas was significant as below canopy populations of macrofauna increased significantly compared to those in other production systems. These data are consistent with those obtained by Durán et al. [61] and Rodríguez et al. [12] who carried out their sampling without considering the effect of the influence of the tree canopy on pastures that are in a certain state of degradation. Therefore, increasing the levels of shade in pastures improves different ecosystem services [26, 62, 63] related mainly to the contribution of biomass [64] (quantity and chemical composition), microclimatic conditions [62, 65] (humidity and temperature) that affect the richness and density of the soil macrofauna community [66]. In this sense, increasing the density of trees in pastures specifically in silvopastoral systems increases macrofauna populations [64, 67].

Rhoades [48] states that scattered trees in pastures affect the chemical conditions of the soil, due to the entry of organic matter from leaves, bark, branches, and roots to the soil system, which the soil fauna transforms and decomposes. This effect occurs in the same way for P. guajava with Mg⁺ and K⁺, and for Z. longifolia with K⁺, where the concentration of these elements increases under the area of influence of their crowns. These results agree with those made by Dahlgren et al. [68] in blue oak (Quercus douglasii), by Eldridge and Wong [69] in four species of Eucalyptus sp., in a temperate zone of Australia, by De Boever et al. [70] in an arid ecosystem in Tunisia, with Acacia raddiana trees, and those made by Kooch et al. [71] in the north of Iran. In general, it demonstrates the importance of scattered trees in pastures to increase soil fertility, being this, among other ecosystem services offered by trees in grazing areas [72].

Casals et al. [28] evaluated differences between the effects of legume and non-legume tree species on soil nutrients and carbon reserves in pastures in Nicaragua, finding higher levels of SOC, N, P, K⁺, and Ca²⁺ under the tree cover than in open field pastures, regardless of whether they were legumes or non legumes, concluding that the magnitude of the effect depends more on tree characteristics such as basal area and crown area than on whether or not the species is a legume. Thus, when relating the effect of trees, De Boever et al. [70] found higher concentrations of nutrients in the soil under the crown of the tree: 175% more compared to outside the crown. However, other biotic and abiotic factors have been associated with the effects of individual plants on soil properties, such as plant species [73], age [70], topography [74], soil texture [75] and functional traits of the tree species [29, 76] and the rate of fall and decomposition of litter [77, 78]. In other types of ecosystems Avendaño-Yáñez et al. [79], Kumar et al. [80], and Mohammed et al. [81] observed that trees improve the fertility of soils under their crowns. We found a significant increase in exchangeable potassium under crown Psidium guajava and Zygia longifolia.

The high values of soil bulk density observed under the crown of some species (A. inermis and Z. longifolia) are mainly due to the use given by the animals as resting areas, where the soil receive a pressure of 1.2 to 1.6 kg cm⁻² [82]. This increase in soil bulk density was related to high values in soil resistance to penetration under its crown. Comparing our results with those presented by Frost and Edinger [83] and Dahlgren et al. [68] they report that they were lower bulk density values. These differences are probably due to the continuous stocking as well as the tree species found in the paddocks referenced in the previous studies. For example, Frost
and Edinger [83] report lower bulk density values under *Quercus wislizenii* crowns than in open grasslands, as well as Dahlgren et al. [68] who investigated the *Quercus douglasii* species under different management combinations: *Q. douglasii* with stocking, *Q. douglasii* without stocking, open grasslands with stocking and open grasslands without stocking; where the soils that are under the crown of *Q. douglasii* presented a lower value of bulk density. Likewise, Tate et al. [84] found that crown cover by any tree species they evaluated in their research significantly reduced the bulk density of the soil surface (16 to 22%) compared to open grasslands. Kumar et al. [80] in an arid region found that the bulk density values under three species (*Prosopis cineraria*, *Acacia Senegal*, and *Tecomella undulata*) were lower than in the open field. Differences observed in bulk density from the studies here cited might be the result of different climatic conditions driving the behaviour of the animal occupying the paddocks thus causing different compaction patterns. *A. inermis* and *Z. longifolia* are tree species that have dense and large crowns that provide areas of greater shade at ground level, allowing grazing cattle to seek these thermoregulation zones to lower body temperature due to high temperature that occurs in the study area (25.5˚C). Moreover, the animals seek the grasses that grow under these areas for their nutritional quality and sometimes the forage (leaves, flowers, and fruits) provided by the trees. Similarly, another factor that can affect this physical variable is the precipitation in the study area (3,793 mm).

Wilson [85] found that along 20 m long transects extending from the crown of trees of the *Eucalyptus melliodora*, *Eucalyptus blakelyi*, and *Eucalyptus nova-anglica* species, the bulk density increased significantly as distance increased relative to the canopies of the trees. In contrast, Kooch et al. [71] in an agroecosystem different from this research work, evaluated the bulk density affected by trees in a mixed forest in Northern Iran, finding an increase in the bulk density of the soil under trees of the *Carpinus betulus* species, due to the low presence of SOM in the soil.

The species *A. inermis* and *Z. longifolia* are trees that have morphological and crown characteristics that allow greater shade at ground level. This allows pastures to have a high concentration of animals in shady sites, negatively affecting the physical properties of the soil and especially the bulk density with high levels of compaction. This can lead to a reduction in root density [86] as well as the volume of soil pores and consequently, the infiltration of water [87, 88] at different depths of the soil. This explains the results found in this work, where the percentage values of soil moisture were higher outside the tree crown than under it.

Stocking density in our study was two animals ha$^{-1}$. Schmalz et al. [89] found an increment in the penetration resistance when comparing paddocks with different stocking densities, penetration resistance was higher in paddocks with 1.56 animals ha$^{-1}$ compared to those with 0.52 animals ha$^{-1}$. Additionally, Greenwood & McKenzie [88] concluded that a stocking density of 1.9 to 2.4 animals ha$^{-1}$ increases compaction and bulk density and decreases soil infiltration in the first 20 cm. Consequently, farm management decisions must take into consideration stocking density [89], particularly in climatic regions were animals due to high temperatures tend to seek refuge under the tree crowns increasing compaction.

We provide evidence that the diversity and density of macrofaunal populations change under the canopy as well as at the tree species level. Thus, increasing shade canopies in paddocks increases the sustainability of livestock production systems. Trees in paddocks provide favorable conditions for macrofauna by increasing the amount of leaf litter in the soil, as well as the chemical composition of the litter [90]. Therefore, as evidenced by the results of the co-inertia analysis, by increasing macrofauna populations there is a significant effect on soil chemical (available P, K, Na, CEC, pH, Al saturation) and soil physical characteristics (bulk density, soil moisture and penetration resistance). Results from this study also demonstrated
how trees in the grazing areas of the pastures in the Colombian Amazon increased some regulation of ecosystem through improved soil fertility [91].

Supporting information
S1 File. Physical, chemical, and biological variables of soil in grazing areas. (XLSX)

Author Contributions
Conceptualization: Faver Álvarez, Fernando Casanoves, Juan Carlos Suárez.
Data curation: Faver Álvarez, Fernando Casanoves, Juan Carlos Suárez.
Formal analysis: Faver Álvarez, Fernando Casanoves, Juan Carlos Suárez.
Funding acquisition: Faver Álvarez.
Investigation: Faver Álvarez, Juan Carlos Suárez.
Methodology: Faver Álvarez, Juan Carlos Suárez.
Project administration: Faver Álvarez.
Resources: Faver Álvarez.
Software: Fernando Casanoves, Juan Carlos Suárez.
Supervision: Fernando Casanoves, Juan Carlos Suárez.
Validation: Fernando Casanoves, Juan Carlos Suárez.
Visualization: Fernando Casanoves, Juan Carlos Suárez.
Writing – original draft: Faver Álvarez, Fernando Casanoves, Juan Carlos Suárez.
Writing – review & editing: Faver Álvarez, Fernando Casanoves, Juan Carlos Suárez.

References
1. IGAC. Estudio general de suelos y zonificación de tierras departamento de Caquetá escala 1:100 000. Imprenta N. Bogotá D.C.; 2014. 415 p.
2. Rodríguez C.H., Blanco J.C., Betancourt B., & Caicedo DF. La situación ambiental del departamento de Caquetá. In: Balance anual sobre el estado de los ecosistemas y el ambiente de la amazonia colombiana 2006. Instituto. Bogotá; 2007. p. 146–54.
3. Ramírez Pava BL, Lavelle P, Orjuela JA, Villanueva O. Characterization of cattle farms and adoption of agroforestry systems as a proposal for soil management in Caquetá, Colombia. Rev Colomb Ciencias Pecu. 2012; 25(3):391–401.
4. FAO. Ganadería y deforestación. Subdirección de Información Ganadera y Sector, De Análisis y Política del Animal. Dirección de Producción y Sanidad [Internet]. Vol. 3, Políticas Pecuarias. 2014 [cited 2021 Mar 22]. Available from: www.lead.virtualcentre.org.
5. Alegre JC, Pashanasiri B, Lavelle P. Dynamics of Soil Physical Properties in Amazonian Agroecosystems Inoculated with Earthworms. Soil Sci Soc Am J. 1996 Sep; 60(5):1522–9.
6. Chauvel A, Grimaldi M, Barros E, Blanchart E, Desjardins T, Sarrazin M, et al. Pasture damage by an Amazonian earthworm. Nature [Internet]. 1999 [cited 2020 Nov 2]; 398(6722):32–3. Available from: https://www.nature.com/articles/17946.
7. McGrath DA, Smith CK, Gholz HL, Oliveira FDA. Effects of land-use change on soil nutrient dynamics in Amazonia. Vol. 4, Ecosystems. Springer; 2001. p. 625–45.
8. Mathieu J, Rossi JP, Mora P, Lavelle P, Martins PF da S, Rouland C, et al. Recovery of Soil Macrofauna Communities after Forest Clearance in Eastern Amazonia, Brazil. Conserv Biol. 2005 Oct; 19(5):1598–605.
9. Lavelle P, Pashanasi B. Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). Pedobiologia (Jena) [Internet]. 1989 [cited 2021 Mar 22]; 33(5):283–92. Available from: https://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=6701033.

10. Sileshi G, Mafongoya PL, Chintu R, Akininfesi FK. Mixed-species legume fallows affect faunal abundance and richness and N cycling compared to single species in maize-fallow rotations. Soil Biol Biochem [Internet]. 2008 [cited 2021 Mar 22]; 40(12):3065–75. Available from: https://www.sciencedirect.com/science/article/pii/S0038071708003155.

11. De Deyn GB, Quirk H, Bardgett RD. Plant species richness, identity and productivity differentially influence key groups of microbes in grassland soils of contrasting fertility. Biol Lett [Internet]. 2011 Feb 23 [cited 2021 Mar 22]; 7(1):75–8. Available from: https://royalsocietypublishing.org/doi/abs/https://doi.org/10.1098/rsbl.2010.0575 PMID: 20685699

12. Rodríguez SL, Paladines JY, AS, Lopez CC, Durán BE, Suárez-Salazar JC. Soil macrofauna under different land uses in the Colombian Amazon. Pesqui Agropecu Bras. 2018 Dec 1; 53(12):1383–91.

13. Hättenschwiler S, Gasser P. Soil animals alter plant litter diversity effects on decomposition. Proc Natl Acad Sci U S A [Internet]. 2005 [cited 2021 Mar 22]; 102(5):1519–24. Available from: www.pnas.org/cgi/doi/10.1073/pnas.0404977102. PMID: 15671172

14. Velásquez E, Fonte SJ, Barot S, Grimaldi M, Desjardins T, Lavelle P. Soil macrofauna-mediated impacts of plant species composition on soil functioning in Amazonian pastures. Appl Soil Ecol [Internet]. 2012 [cited 2019 Jul 27]; 56:43–50. Available from: https://www.sciencedirect.com/science/article/pii/S0929139312000200.

15. Ristok C, Leppert KN, Scherer-Lorenzen M, Niklaus PA, Bruelheide H. Soil macrofauna and leaf functional traits drive the decomposition of secondary metabolites in leaf litter. Soil Biol Biochem [Internet]. 2019 [cited 2021 Mar 22]; 135:429–37. Available from: https://www.sciencedirect.com/science/article/pii/S003807171930166X.

16. Guendehou GHS, Liski J, Tuomi M, Moudachirou M, Sinsin B, Måkippä R. Decomposition and changes in chemical composition of leaf litter of five dominant tree species in a West African tropical forest. Trop Ecol [Internet]. 2014 [cited 2021 Mar 22]; 55(2):207–20. Available from: https://www.academia.edu/download/43106375/Tropical_Ecology_552_207-220_2014_Deco20160226-24262-16660oo.pdf.

17. Gartzia-Bengoetxea N, Kandelé E, Martínez de Arano I, Arias-González A. Soil microbial functional activity is governed by a combination of tree species composition and soil properties in temperate forests. Appl Soil Ecol [Internet]. 2016 [cited 2021 Mar 22]; 100:57–64. Available from: https://www.sciencedirect.com/science/article/pii/S0929139315301293.

18. Siqueira FF, Calasans LV, Furtado RQ, Carneiro VMC, van den Berg E. How scattered trees matter for biodiversity conservation in active pastures. Agric Ecosyst Environ. 2017 Dec 1; 250:12–9.

19. Mancera KF, Zarza H, de Buen LL, García AAC, Palacios FM, Galindo F. Integrating links between tree coverage and cattle welfare in silvopastoral systems evaluation. Agron Sustain Dev. 2018 Apr 1; 38(2).

20. Álvarez F, Casanoves F, Suárez JC, Pezo D. The effect of different levels of tree cover on milk production in dual-purpose livestock systems in the humid tropics of the Colombian Amazon region. Agrofor Syst [Internet]. 2020 Nov 5 [cited 2020 Nov 15]:1–10. Available from: https://link.springer.com/article/10.1007/s10457-020-00566-7.

21. Ibrahim M, Canto G, Camero A. Establishment and management of fodder banks for livestock feeding in Cayo. Agroforestry prototypes for Belize. Turrialba, Costa Rica, CATIE-GTZ, 15–39. 1998.

22. Gómez R, López M. Caracterización de las fincas ganaderas y relación con la cobertura arbórea en los sistemas ganaderos de Rivas, Nicaragua. Nitlapán-Universidad Centroamericana. Nicaragua. 2004.

23. Luis Martínez-Sánchez J. Pasture trees in tropical México: the effect of soil nutrients on seedling growth. Vol. 54, Rev. Biol. Trop. (Int. J. Trop. Biol.) ISSN. 2006.

24. Cezar RM, Vezzani FM, Schwiderke DK, Gaiad S, Brown GG, Seoane CES, et al. Soil biological properties in multistage successional agroforestry systems and in natural regeneration. Agrofor Syst. 2015 Jul 30; 89(6):1035–47.

25. Suárez LR, Suárez Salazar JC, Casanoves F, Ngo Bieng MA. Cacao agroforestry systems improve soil fertility: Comparison of soil properties between forest, cacao agroforestry systems, and pasture in the Colombian Amazon. Agric Ecosyst Environ [Internet]. 2021 Jul 1 [cited 2021 Mar 22]; 314:107349. Available from: https://linkinghub.elsevier.com/retrieve/pii/S0167880921000530.

26. Rodríguez L, Suárez JC, Pulleman M, Guaca L, Rico A, Romero M, et al. Agroforestry systems in the Colombian Amazon improve the provision of soil ecosystem services. Appl Soil Ecol [Internet]. 2021 [cited 2021 Mar 22];164. Available from: https://www.sciencedirect.com/science/article/pii/S0929139321000548.

27. Santos PZF, Crouzeilles R, Sansevero JBB. Can agroforestry systems enhance biodiversity and ecosystem service provision in agricultural landscapes? A meta-analysis for the Brazilian Atlantic Forest.
For Ecol Manage [Internet]. 2019 [cited 2021 Mar 22]; 433:140–5. Available from: https://www.sciencedirect.com/science/article/pii/S037811271831332X.

28. Casals P, Romero J, Rusch GM, Ibrahim M. Soil organic C and nutrient contents under trees with different functional characteristics in seasonally dry tropical silvopastures. Plant Soil [Internet]. 2014 Jan 1 [cited 2021 Mar 22]; 374(1–2):643–59. Available from: https://link.springer.com/article/10.1007/s11104-013-1884-9.

29. Lana AMQ, Lana RMQ, Lemes EM, Reis GL, Moreira GHFA. Influence of native or exotic trees on soil fertility in decades of silvopastoral system at the Brazilian savannah biome. Agrofor Syst. 2018 Apr 1; 92(2):415–24.

30. Esquivel MJ, Harvey CA, Finegan B, Casanoves F, Skarpe C. Effects of pasture management on the natural regeneration of neotropical trees. J Appl Ecol [Internet]. 2008 Feb [cited 2021 Mar 22]; 45(1):371–80. Available from: https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2664.2007.01411.x.

31. Gutiérrez García GA, Suárez Salazar JC, Álvarez Carrillo F, Orjuela Chaves JA. Árboles dispersos en potreros y conectividad estructural en el paisaje de fincas ganaderas en la Amazonia Colombiana. Ing Amaz [Internet]. 2012 [cited 2021 Mar 22]; 5(1):30–41. Available from: https://www.uniamazonia.edu.co/revistas/index.php/ingenierias-y-amazonia/article/view/98.

32. Rusch GM, Zapata PC, Casanoves F, Casals P, Ibrahim M, Declerck F, et al. Determinants of grassland primary production in seasonally-dry silvopastoral systems in Central America. Agroforest Syst [Internet]. 2014 [cited 2021 Mar 22]; 88:517–26. Available from: https://link.springer.com/content/pdf/10.1007/s10457-014-9711-8.pdf.

33. Köppen W. Ges. geographischen system der klimate. En: Köppen, W. y Geiger, R. Handbuch der klimatologie. Bohntraeger. Berlin. 1938.

34. Holdridge L. Ecología basada en zonas de vida. IICA. San José, Costa Rica. 216. 1978.

35. Álvarez F, Casanoves F, Suarez J, Calderón V, Ngo BM, Ruch G. The structure of dispersed trees in livestock farmers of the colombian amazon and its relationship with local knowledge. 2021.

36. ISO. 23611–5. Soil quality- Sampling of soil invertebrates-Part 5: Sampling and extraction of soil macro-invertebrates. 2011.

37. Walkley A, Black IA. An examination of the determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci. 1934; 37(1):29–38.

38. Heaton L, Fullen MA, Bhattacharyya R. Critical Analysis of the van Bemmelen Conversion Factor used to Convert Soil Organic Matter Data to Soil Organic Carbon Data: Comparative Analyses in a UK Loamy Sand Soil. Espacio Aberto [Internet]. 2016 [cited 2021 May 20]; 6(1):35–44. Available from: https://revistas.ufrj.br/index.php/espacioAberto/article/viewFile/5244/3852.

39. Mehlich A. Mehlich 3 Soil Test Extractant: A Modification of Mehlich 2 Extractant. Commun Soil Sci Plant Anal. 1984 Dec 1; 15(12):1409–16.

40. Lax A, Roig A, Costa F. A method for determining the cation-exchange capacity of organic materials. Plant Soil [Internet]. 1986 [cited 2021 Mar 22]; 94(3):349–55. Available from: https://www.sciencedirect.com/science/article/pii/S0010498186800985.

41. Olsen S., Cole C., Wantanabe F., Dean LA. (1954). Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circular 939. U.S. Government Printing Office, Washington DC. 1954.

42. Kuo S. Phosphorus. In: Sparks DL, AL Page, PA Helmke, RH Loeppert, PN Soltanpour, MA Tabatabai, MS pp., editor. Methods of soil analysis Part 3 Chemical methods. Soil Science Society of America Inc., Madison, WI. 1996. p. 869–916.

43. Murphy J, Riley JP. A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta [Internet]. 1962 [cited 2021 Mar 22]; 27(C):31–6. Available from: https://www.sciencedirect.com/science/article/pii/S0003267000884445.

44. Blake GR, Hartge KH. Particle density In: Klute A., editor,. In: Methods of Soil Analysis: Part 1—Physical and Mineralogical Methods [Internet]. John Wiley & Sons, Ltd; 1986 [cited 2020 Jun 14]. p. 504–5. Available from: http://doi.wiley.com/10.2136/sssabookser5.1.2ed.c14.

45. Di Rienzo JA, Macchiavel R, Casanoves F. Modelos lineales generalizados mixtos: Aplicaciones en InfoStat. ISBN 978-987-42-4985-2. 2017.

46. Di Rienzo J, Casanoves F, Balzarini M, González L. InfoStat versión 2019. Centro de Transferencia InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. URL http://www.infostat.com.ar. 2019.

47. R Development Core Team. R: The R Project for Statistical Computing. In: Foundation for Statistical Computing, V., Austria. ISBN 3-900051-07-0 (Ed.). 2021; Available from: https://www.r-project.org/.

48. Rhoades CC. Single-tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. Agrofor Syst. 1996; 35(1):71–94.
49. Korboulewsky N, Perez G, Chauvat M. How tree diversity affects soil fauna diversity: A review [Internet]. Vol. 94, Soil Biology and Biochemistry. 2016 [cited 2021 Mar 22]. p. 94–106. Available from: https://www.sciencedirect.com/science/article/pii/S0038071715004174.

50. Kamau S, Barrios E, Karanja NK, Ayuke FO, Lehmann J. Soil macrofauna abundance under dominant tree species increases along a soil degradation gradient. Elsevier [Internet]. 2017 [cited 2021 Mar 22]; Available from: http://dx.doi.org/10.1016/j.soilbio.2017.04.016.

51. Vohland K, Schroth G. Distribution patterns of the litter macrofauna in agroforestry and monoculture plantations in central Amazonia as affected by plant species and management. Appl Soil Ecol [Internet]. 1999 [cited 2021 Mar 22]; 13(1):57–68. Available from: https://www.sciencedirect.com/science/article/pii/S0929139399000219.

52. Gholami S, Sheikhmohamadi B, Sayad E. Spatial relationship between soil macrofauna biodiversity and trees in Zagros forests, Iran. Catena [Internet]. 2017 [cited 2021 Mar 22]; 159:1–8. Available from: https://www.sciencedirect.com/science/article/pii/S0009898116307450.

53. Laossi KR, Barot S, Carvalho D, Desjardins T, Lavelle P, Martins M, et al. Effects of plant diversity on plant biomass production and soil macrofauna in Amazonian pastures. Pedobiologia (Jena) [Internet]. 2008 [cited 2021 Mar 22]; 51(5–6):397–407. Available from: www.elsevier.de/pedobi.

54. Wilson J., Ludlow M. The environment and potential growth of herbage under plantations. (ed. Shelton HMand Sturr WW) Australian Centre for International Agricultural Research Proceedings series, 32. In: Forages for Plantation Crops. 1991. p. 10–24.

55. Reynolds S. Pasture–Cattle–Coconuts Systems. FAO/ RAPA Publication 1995/7. Regional Office for Asia and the Pacific, FAO, Bangkok, Thailand. 668. 1995.

56. Reynolds S. Pasture–Cattle–Coconuts Systems. FAO/ RAPA Publication 1995/7. Regional Office for Asia and the Pacific, FAO, Bangkok, Thailand. 668. 1995.

57. Lott JE, Ong CK, Black CR. Understorey microclimate and crop performance in a Grevillea robusta-based agroforestry system in semi-arid Kenya. Elsevier [Internet]. [cited 2021 Mar 22]; Available from: https://www.sciencedirect.com/science/article/pii/S016788090001444.

58. Lott JE, Ong CK, Black CR. Understorey microclimate and crop performance in a Grevillea robusta-based agroforestry system in semi-arid Kenya. Agric For Meteorol [Internet]. 2009 [cited 2021 Mar 22]; 149(6–7):1140–51. Available from: https://www.sciencedirect.com/science/article/pii/S0168192309000144.

59. Lott JE, Ong CK, Black CR. Understorey microclimate and crop performance in a Grevillea robusta-based agroforestry system in semi-arid Kenya. Agric For Meteorol [Internet]. 2009 [cited 2021 Mar 22]; 149(6–7):1140–51. Available from: https://www.sciencedirect.com/science/article/pii/S0168192309000144.

60. Tsiafouli MA, Kallimanis AS, Katana E, Stamou GP, Sgardelis SP. Responses of soil microarthropods to experimental short-term manipulations of soil moisture. Appl Soil Ecol [Internet]. 2005 [cited 2021 Mar 22]; 29(1):17–26. Available from: https://www.sciencedirect.com/science/article/pii/S0929139304001295.

61. Tsiatouli MA, Kallimanis AS, Katana E, Stamou GP, Sgardelis SP. Responses of soil microarthropods to experimental short-term manipulations of soil moisture. Appl Soil Ecol [Internet]. 2005 [cited 2021 Mar 22]; 29(1):17–26. Available from: https://www.sciencedirect.com/science/article/pii/S0929139304001295.

62. Paiva IG, Auad AM, Verissimo BA, Silveira LCP. Differences in the insect fauna associated to a monocultural pasture and a silvopasture in Southeastern Brazil. Sci Reports 2020 101 [Internet]. 2020 Jul 21 [cited 2021 Sep 9]; 10(1):1–16. Available from: https://www.nature.com/articles/s41598-020-68973-5. https://doi.org/10.1038/s41598-020-68973-5 PMID: 32694546

63. Lavelle P, Délolé P, de Sartre XA, Decaëns T, Gond V, Grimaldi M, et al. Unsustainable landscapes of deforested Amazonia: An analysis of the relationships among landscapes and the social, economic and environmental profiles of farms at different ages following deforestation. Glob Environ Chang. 2016 Sep; 40:137–55.

64. Teutschckerová N, Vázquez E, Sotelo M, Villegas D, Velásquez N, Baquero D, et al. Intensive short-duration rotational grazing is associated with improved soil quality within one year after establishment in Colombia. Appl Soil Ecol. 2021 Mar 1; 159:103835.

65. Vieira FMC, Pilatti JA, Czekoski ZMW, Fonseca VFC, Herbut P, Angrecka S, et al. Effect of the Silvo-pastoral System on the Thermal Comfort of Lambs in a Subtropical Climate: A Preliminary Study. Agriculture [Internet]. 2021 Aug 19 [cited 2021 Sep 9]; 11(8):790. Available from: https://www.mdpi.com/2077-0472/11/8/790/htm.
66. Vazquez E, Teutschcherova N, Lojka B, Arango J, Pulleman M. Pasture diversification affects soil macrofauna and soil biophysical properties in tropical (silvo)pastoral systems. Agric Ecosyst Environ. 2020 Oct 15; 302:107083.

67. Giraldo C, Escobar F, Chará JD, Calle Z. The adoption of silvopastoral systems promotes the recovery of ecological processes regulated by dung beetles in the Colombian Andes. Insect Conserv Divers [Internet]. 2011 May 1 [cited 2021 Sep 9]; 4(2):115–22. Available from: https://onlinelibrary.wiley.com/doi/full/10.1111/j.1752-4598.2010.00112.x.

68. Dahlgren RA, Singer MJ, Huang X. Oak tree and grazing impacts on soil properties and nutrients in a california oak woodland. Biogeochemistry. 1997; 39(1):45–64.

69. Eldridge DJ, Wong VNL. Clumped and isolated trees influence soil nutrient levels in an Australian temperate box woodland. Plant Soil [Internet]. 2005 Mar [cited 2021 Mar 22]; 270(1):331–42. Available from: https://www.researchgate.net/publication/201997345.

70. De Boever M, Gabriels D, Oues sar M, Cornelis W. Influence of scattered Acacia trees on soil nutrient levels in arid Tunisia. J Arid Environ [Internet]. 2015 [cited 2021 Mar 22]; 122:161–8. Available from: https://www.sciencedirect.com/science/article/pii/S01401963000105X.

71. Kooch Y, Samadzadeh B, Hosseini SM. The effects of broad-leaved tree species on litter quality and soil properties in a plain forest stand. Catena [Internet]. 2017 [cited 2021 Mar 22]; 150:223–9. Available from: https://www.sciencedirect.com/science/article/pii/S0341816216305021.

72. Graham S, Wilson BR, Reid N, Jones H. Scattered paddock trees, litter chemistry, and surface soil properties in pastures of the New England Tablelands, New South Wales. Aust J Soil Res [Internet]. 2004 Dec 16 [cited 2021 May 20]; 42(8):905–12. Available from: https://www.publish.csiro.au/sr/SR03065.

73. Li J, Zhao C, Zhu H, Li Y, Wang F. Effect of plant species on shrub fertile island at an oasis-desert ecosystem in the South Junggar Basin, China. J Arid Environ [Internet]. 2007 [cited 2021 Mar 22]; 71(4):350–61. Available from: https://www.sciencedirect.com/science/article/pii/S0140196307000985.

74. Harman CJ, Lohse KA, Troch PA, Sivapalan M. Spatial patterns of vegetation, soils, and microtopography from terrestrial laser scanning on two semiarid hillslopes of contrasting lithology. J Geophys Res Biogeosciences [Internet]. 2014 [cited 2021 Mar 22]; 119(2):163–80. Available from: https://www.czo.arizona.edu.

75. Wei X, Shao M, Fu X, Horton R. Changes in soil organic carbon and total nitrogen after 28 years grassland afforestation: Effects of tree species, slope position, and soil order. Plant Soil. 2010 Jun; 331 (1):165–79.

76. Casanovas F, Pla L, Di Rienzo JA. Diversidad funcional Valoración y análisis de la diversidad funcional y su relación con los servicios ecosistémicos. 2011. 105 p. PMID: 22017136

77. Lanuza O, Casanoves F, Delgado D, Van den Meersche K. Leaf litter stoichiometry affects decomposition rates and nutrient dynamics in tropical forests under restoration in Costa Rica. Restor Ecol. 2019 May 1; 27(3):549–58.

78. Lanuza O, Casanoves F, Zahawi RA, Celentano D, Delgado D, Holl KD. Litterfall and nutrient dynamics shift in tropical forest restoration sites after a decade of recovery. Wiley Online Libr [Internet]. 2018 May 1 [cited 2021 Mar 22]; 50(3):491–8. Available from: https://onlinelibrary.wiley.com/doi/abs/10.1111/btep.12533.

79. Avendaño-Yáñez M de la L, López-Ortiz S, Perroni Y, Pérez-Elizalde S. Leguminous trees from tropical dry forest generate fertility islands in pastures. Arid Land Res Manag [Internet]. 2018 Jan 2 [cited 2021 Mar 22]; 32(1):57–70. Available from: https://www.tandfonline.com/doi/abs/10.1080/15324982.2017.1377782.

80. Kumar A, Dorodnikov M, Splettstößer T, Kuzyakov Y, Pausch J. Effects of maize roots on aggregate stability and enzyme activities in soil. Geoderma [Internet]. 2017 Nov 15 [cited 2019 Jul 27]; 306:50–70. Available from: https://www.sciencedirect.com/science/article/pii/S0016706116306836.

81. Musa M, Ebro A, Nigatu L. Impact of woody plants species on soil physico-chemical properties along grazing gradients in rangelands of eastern Ethiopia. Trop Subtrop Agroecosystems [Internet]. 2016 [cited 2021 Mar 22]; 19(3):343–55. Available from: https://www.revista.ccca.uady.mx/ojs/index.php/ TSA/article/view/2254.

82. Pearson CJ, Ison RL. Agronomy of grassland systems. Cambridge University Press. 1997.

83. Frost WE, Edinger SB. Effects of tree canopies on soil characteristics of annual rangeland. J Range Manag [Internet]. 1991 [cited 2021 Mar 22]; 44(3):266–8. Available from: https://journals.uaarizona.edu/index.php/jrm/article/view/8666.

84. Tate KW, Dudley D, McDonalld N. Title Effect of Canopy and Grazing on Soil Bulk Density Publication Date [Internet]. Vol. 57, Journal Journal of Range Management. 2004 [cited 2021 Mar 22]. Available from: https://escholarship.org/uc/item/0m9815mh.
85. Wilson B. Influence of scattered paddock trees on surface soil properties: A study of the Northern tablelands of NSW. Ecol Manag Restor [Internet]. 2002 Dec [cited 2021 Mar 22]; 3(3):211–9. Available from: https://www.researchgate.net/publication/229944414.

86. Sinnett D, Morgan G, Williams M, Hutchings TR. La resistencia a la penetración del suelo y el desarrollo de la raíz del árbol. Uso y manejo del suelo. 2008; 24(3):273–80.

87. Pezo D, Romero F, Ibrahim M. Producción, manejo y utilización de los pastos tropicales para la producción de leche y carne. Avances en la producción de leche y carne en el trópico americano, FAO, Santiago de Chile, 47–98. In: Fernández-Baca, editor. 1992.

88. Greenwood KL, McKenzie BM. Grazing effects on soil physical properties and the consequences for pastures: A review [Internet]. Vol. 41, Australian Journal of Experimental Agriculture. 2001 [cited 2021 Mar 22]. p. 1231–50. Available from: http://www.publish.csiro.au/AN/EA00102.

89. Schmalz HJ, Taylor R V., Johnson TN, Kennedy PL, Debano SJ, Newingham BA, et al. Soil Morphologic Properties and Cattle Stocking Rate Affect Dynamic Soil Properties. Rangel Ecol Manag. 2013 Jul 1; 66(4):445–53.

90. Piza PA, Suárez JC, Andrade HJ. Litter decomposition and nutrient release in different land use located in Valle del Cauca (Colombia). Agrofor Syst [Internet]. 2021 Jan 3 [cited 2021 Sep 9]; 95(2):257–67. Available from: https://link.springer.com/article/10.1007/s10457-020-00583-6.

91. Trilleras JM, Jaramillo VJ, Vega E V., Balvanera P. Effects of livestock management on the supply of ecosystem services in pastures in a tropical dry region of western Mexico. Agric Ecosyst Environ. 2015 Dec 15; 211:133–44.