

## Biogeographical and edaphic drivers of earthworm assemblages in Guyana

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### Abstract

Earthworms serve as vital bioindicators of soil health and are significant regulators of soil structure and organic matter dynamics in terrestrial ecosystems. In the face of intensifying anthropogenic pressures on soils and global climate, earthworm populations are increasingly vulnerable to the strains imposed by agriculture, mining, and deforestation. This study aimed to characterise earthworm assemblage structure across Guyana and to evaluate the influence of biogeographical, climatic, and edaphic factors on earthworm communities and ecotype distribution. Earthworms and soil samples were collected from 60 sites. Earthworms were methodologically dissected to aid in their identification, and soil samples were analysed for 16 parameters. A total of 68 morpho-species of earthworms from 8 families were identified. Of the four biogeographical regions, the Highland Region exhibited the highest diversity, species richness and abundance. Statistical analysis revealed that soil, habitat and biogeography significantly influenced earthworm abundance and distribution of ecotypes. Soil analysis revealed that earthworm abundance was significantly correlated with soil calcium ( $R^2 = 0.07$ ,  $p = 0.006$ ), phosphorus ( $R^2 = 0.06$ ,  $p = 0.006$ ) and iron ( $R^2 = 0.05$ ,  $p = 0.016$ ). Endo-anecic abundance was negatively correlated with calcium (-1.6) and iron (-1.8) and anecic abundance was positively correlated with phosphorus (+1.1) and negatively correlated with calcium (-1.1). Multivariate analysis revealed that soil type ( $R^2 = 0.39$ ,  $p < 0.001$ ), habitat type ( $R^2 = 0.19$ ,  $p = 0.011$ ) and geography ( $R^2 = 0.16$ ,  $p < 0.001$ ) were the most significant drivers of the ecotype composition of earthworm communities. These findings provide a critical baseline for understanding the edaphic and climatic filters that shape soil biodiversity in the Guiana Shield and reinforce the sensitivity of specific ecotypes to land-use changes.

**Key words:** biogeography, climate, earthworms, ecotypes, edaphic factors.

### Introduction

Guyana is a highly biodiverse Amazonian country with four distinct biogeographical regions, each of which has unique soils, habitats and climates (Guyana Lands & Surveys Commission 2026). This bioge-

graphic and climatic variability represents important vicariance forces leading to speciation and distinct plant and animal communities (Hua and Wiens 2013). Additionally, significant economic activities in the country such as mining, agriculture and logging, can threaten local soil health, soil

biodiversity and the ecosystem services they provide (Southwell and Majer 1982, Rao 2013). To avoid soil health crisis, efforts must be placed into maintaining soil biodiversity, and the services it provides, by promoting sustainable management practices and conservation.

Soil invertebrates represent approximately 23 % of the world's species (Decaëns et al. 2006, Anthony et al. 2023), and among these earthworms stand out as major players due to their widely recognised ecosystem services and importance in agriculture. Hence, they have been widely used as bioindicators of soil health in monitoring programs, especially in Europe (Bünemann et al. 2018). Earthworms are important ecosystem engineers that modify the physical structure of soil through the formation of macro-aggregates and pores (Chauhan 2014). They play an active role in maintaining soil fertility by burrowing and casting and moving nutrients through the soil profile (Akhila and Entoori 2022).

Nevertheless, the ecological role of earthworms is not the same for all species. They can be classified into three ecological groups, each of which carries out specific functions (Bottinelli et al. 2020). The pigmented epigeic species live on the soil surface and are heavily involved in decomposition. The dorsally pigmented anecic species are deep burrowers that move nutrients through the soil profile, promoting incorporation of surface residues and their decomposition. Finally, the unpigmented endogeic species reside primarily in the soil and by eating large quantities of soil, promote the release of inorganic nutrients (Edwards and Bohlen 1996, Lal 2007, Sherameti and Varma 2015).

Earthworm community structure and composition is largely influenced by climate, particularly temperature; however,

geography, unique microclimates, biotic interactions and land conversion can significantly influence community composition particularly in tropical ecosystems, where conversions lead to habitat homogenisation, simplifying communities (Lavelle 1983, Phillips et al. 2019). Furthermore, physical and chemical changes to the soil can alter earthworm communities, and properties such as texture, moisture and nutrient contents can affect their abundance and distribution (Nuutinen et al. 1998, Bohlen et al. 2004, Edwards 2004).

In the present study we characterised earthworm assemblages across Guyana and evaluated the influence of biogeographical, climatic, and edaphic factors on community composition and ecotype distribution by testing three hypotheses: (1) Differences in earthworm assemblage structure will occur among biogeographical regions; (2) Earthworm abundance will be influenced by biogeographical and environmental factors; (3) Assemblage structure will correlate with soil physico-chemical properties.

## Materials and Methods

### Description of study area

This study was conducted in 60 sites in Guyana, chosen and classified based on their climate, habitat, and soil type (Table 1, Fig. 1). Köppen classification system (Peel et al. 2007) was used to determine the climate type – the northern half of the country displays an equatorial climate, the southern half a tropical savannah climate, while the central region displays a monsoon climate.

The habitat type was determined following the classification system of the Guyana Forestry Commission (2012),

which led to the observation of 6 distinct types: mixed forest, wallaba/dacama forest, montane forest, mangrove forest, savanna, and grassland. The soil type was classified according to the FAO classification system and soil map of South America (FAO 1971, FAO 1998), which revealed the following soil types: Acrisol, Aerenosol, Anthrosol, Ferralsol, Lixisol, Gleysol, Histosol, and Leptosol.

### Experimental design and earthworm sampling

Fifteen sampling sites were randomly established within each of the four biogeographical regions (Low Coastal Plain, Hilly Sand and Clay Region, Highland Region, and Interior Savanna), (Fig. 1), classified according to the Guyana Lands & Surveys

Commission (2026). GPS coordinates of each site were recorded (Appendix A, Table A1).

In each of the 60 sites, 15 sampling points were selected along a linear transect at 6 m intervals, where the soil was removed from a pit measuring 0.5 m × 0.5 m, to 0.5 m depth. It was removed by manual digging, after which it was hand-sorted for earthworms, which were then categorised and counted.

### Earthworm identification

Earthworms were separated into morphospecies, based on internal and external morphological features, as well as into adults (with developed clitellum) and juveniles. Two adults from each morphospecies were separately fixed in 95%

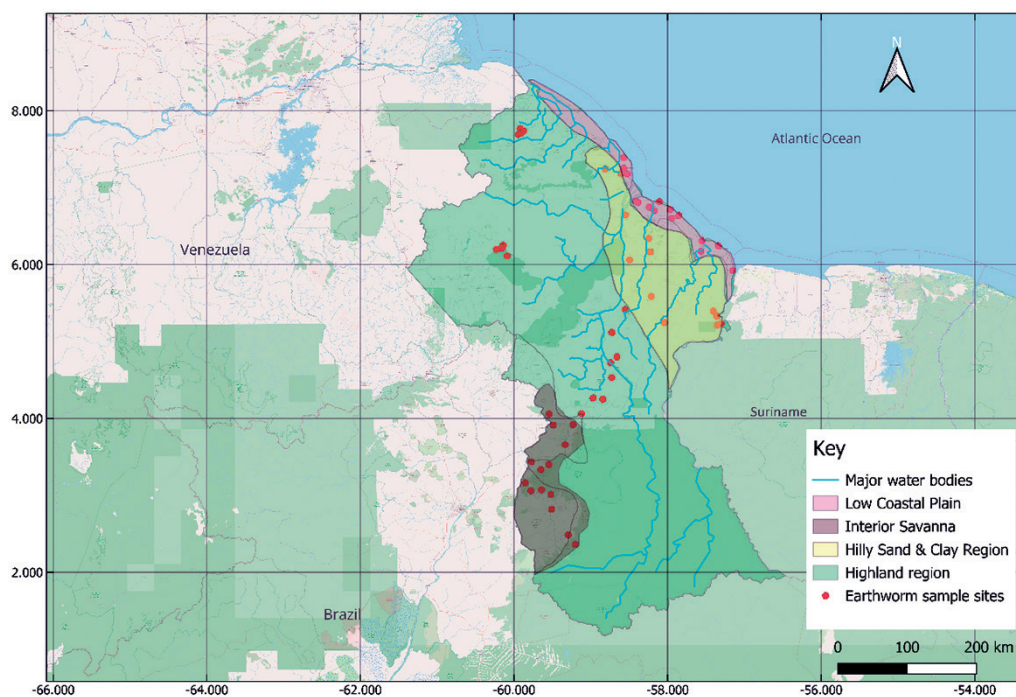


**Fig. 1.** Map of Guyana showing the four biogeographical regions from which the sampling sites were selected. Map created using QGIS (version 3.40.12)

ethanol for dissection. Earthworms were placed in a Petri dish and examined under light microscopy for the following features: circumference, length, and the type, number, and position of key external features: clitellum, segments, prostomium, dorsal and nephridial pores, genital pores and markings, setal length and arrangement. They were then placed in a dissecting tray, dorsal side up, pinned and dissected. A dissecting microscope was then used to determine the number and position of the internal organs: calciferous glands, seminal vesicles, spermatheca, heart and gizzard (Ansari and Saywack 2011). The setae were then isolated using 5% caustic potash and measured using a micrometre. Earthworms were placed into families based on their taxonomic features (Blakemore 2013). Earthworms were categorised into ecological groups (ecotypes) based on coloration, feeding habit and depth of soil occupied (Bottinelli et al. 2020). Epigeic species were the smaller pigmented litter-dwellers. The remaining 4 ecotypes are found within the soil: epi-endogeics were small and moderately pigmented, endo-anecics were larger species with anterior pigmentation, anecics were larger species with dorsal pigmentation and finally, endogeics were unpigmented individuals.

### Assemblage structure

The parameters of earthworm assemblage structure that were assessed in this study include: Hill-Shannon diversity (effective number of species), species richness, relative abundance and ecotype distribution. These were compared across biogeographic regions, climate type, soil type, habitat type, edaphic variables and disturbance.

### Soil analysis

One sample from each site was taken from the middle of the transect and was stored in labelled zip lock bags until analysis. A subsample was removed for soil moisture determination, and the remaining sample was air-dried and sieved at 2 mm for chemical and physical analysis (Hoskins and Ross 2011). Soils were analysed at the National Agricultural Research & Extension Institute (NAREI). Samples were tested for salinity, pH in water, total salts in water extract, organic Carbon (Walkley & Black method), total Kjeldahl Nitrogen, available Bray Phosphate, exchangeable Calcium (in 1M Potassium Chloride extract), exchangeable Potassium, Iron, Copper and Magnesium (in Ammonium Acetate extract), extractable Zinc (DTPA Method), Sulphate content (Wet Chemical Method) and Cation Exchange Capacity (Craze 1990, Homer 2003, The Northeast Coordinating Committee for Soil Testing 2011).

### Statistical analysis

The data was analysed using RStudio (version 4.5.3). ANOVA was used to test for significance in total earthworm abundance across variables –  $p$ -value < 0.05 indicated statistically significant differences. *Post-hoc* Tukey's HSD were then performed and distinct letters were generated at a significance level of ( $\alpha = 0.05$ ).

Ecotype abundance data were transformed using the Hellinger method to account for high variation and 0 counts. A PERMANOVA, using the Bray-Curtis dissimilarity was then used to test the significance ( $p < 0.05$ ) of biogeographical region, habitat, climate, soil and disturbance on ecotype abundance, using

R's vegan package. GLMs were used to identify the ecotypes driving community patterns across the biogeographic regions and *post-hoc* comparisons were extracted using emmeans and multcompView. Soil variables were screened for collinearity using Variance Inflation Factors leading to the pruning of Na, TDS and CEC, and the remaining variables were z-score standardised. Forward stepwise selection was carried out on distance-based Redundancy Analysis models followed by a marginal PERMANOVA (higher  $R^2$  values indicate a stronger influence of edaphic variables). A multivariate GLM was then carried out using a negative binomial distribution.

Hill numbers (Hill-Shannon ( $q = 1$ ) and

species richness ( $q = 0$ )) were calculated using R's iNEXT package and coverage-based rarefaction curves were generated.

## Results

### Taxonomic composition

A total of 68 morpho-species (msp.) of earthworms belonging to 8 families were identified within the study area (Table 1). The family Rhinodrilidae had the highest taxonomic richness (33 msp.), followed by Glossoscolecidae (17 msp.), and Ocnerodrilidae (8 msp.). The remaining 5

**Table 1. Earthworm taxa collected and their relative abundance in the different biogeographic regions of Guyana.**

| Earthworm taxonomy           | Ecotype  | Biogeographic regions |                            |                 |                  |
|------------------------------|----------|-----------------------|----------------------------|-----------------|------------------|
|                              |          | Low Coastal Plain     | Hilly Sand and Clay Region | Highland Region | Interior Savanna |
| Acanthodrilidae              |          |                       |                            |                 |                  |
| <i>Acanthodrilidae</i> sp. 1 | Endogeic | 399                   |                            |                 |                  |
| Almidae family               |          |                       |                            |                 |                  |
| <i>Alma</i> sp.              | Epigeic  |                       | 61                         | 112             |                  |
| <i>Drilocrius</i> sp. 1      | Epigeic  |                       |                            | 105             | 124              |
| <i>Drilocrius</i> sp. 2      | Epigeic  |                       |                            | 6               |                  |
| Benhamiidae family           |          |                       |                            |                 |                  |
| <i>Dichogaster saliens</i>   | Epigeic  | 111                   |                            |                 |                  |
| <i>Dichogaster</i> sp. 1     | Epigeic  | 688                   | 1070                       |                 |                  |
| <i>Dichogaster</i> sp. 2     | Endogeic |                       | 274                        | 1258            | 288              |
| Eudrilidae                   |          |                       |                            |                 |                  |
| <i>Eudrilus</i> sp.          | Epigeic  |                       | 10                         |                 |                  |
| Glossoscolecidae             |          |                       |                            |                 |                  |
| <i>Enantiodrilus</i> sp.     | Endogeic |                       |                            |                 | 97               |
| <i>Glossoscolex</i> sp. 1    | Epigeic  |                       | 182                        |                 |                  |
| <i>Glossoscolex</i> sp. 2    | Endogeic | 433                   |                            |                 |                  |
| <i>Glossoscolex</i> sp. 3    | Endogeic |                       |                            |                 | 568              |
| <i>Glossoscolex</i> sp. 4    | Endogeic | 101                   | 95                         |                 |                  |
| <i>Glossoscolex</i> sp. 5    | Endogeic |                       | 96                         |                 |                  |
| <i>Glossoscolex</i> sp. 6    | Endogeic |                       | 127                        | 52              |                  |

| Earthworm taxonomy         | Ecotype      | Biogeographic regions |                            |                 |                  |
|----------------------------|--------------|-----------------------|----------------------------|-----------------|------------------|
|                            |              | Low Coastal Plain     | Hilly Sand and Clay Region | Highland Region | Interior Savanna |
| <i>Glossoscolex</i> sp. 7  | Endogeic     |                       |                            |                 | 26               |
| <i>Glossoscolex</i> sp. 8  | Anecic       |                       |                            | 198             | 81               |
| <i>Martiodrilus</i> sp. 1  | Anecic       |                       |                            | 216             |                  |
| <i>Martiodrilus</i> sp. 2  | Anecic       | 499                   | 75                         |                 |                  |
| <i>Martiodrilus</i> sp. 3  | Anecic       |                       |                            | 348             |                  |
| <i>Martiodrilus</i> sp. 4  | Anecic       | 11                    |                            |                 |                  |
| <i>Righiodrilus</i> sp. 1  | Epi-endogeic |                       | 315                        | 126             | 203              |
| <i>Righiodrilus</i> sp. 2  | Epi-endogeic | 1422                  |                            |                 |                  |
| <i>Righiodrilus</i> sp. 3  | Epi-endogeic | 681                   |                            | 102             |                  |
| <i>Righiodrilus</i> sp. 4  | Anecic       |                       |                            |                 |                  |
| Megascolecidae             |              |                       |                            |                 |                  |
| <i>Amyntas</i> sp.         | Epigeic      |                       | 75                         |                 |                  |
| <i>Polypheritima</i> sp.   | Endogeic     | 27                    |                            |                 |                  |
| Ocnerodrilidae             |              |                       |                            |                 |                  |
| <i>Eukerria saltensis</i>  | Endogeic     | 205                   |                            |                 |                  |
| <i>Eukerria stagnalis</i>  | Endogeic     | 114                   |                            |                 |                  |
| <i>Ocnerodrilus</i> sp. 1  | Endogeic     |                       |                            | 142             |                  |
| <i>Ocnerodrilus</i> sp. 2  | Endogeic     |                       |                            | 51              |                  |
| <i>Ocnerodrilus</i> sp. 3  | Endogeic     |                       |                            | 221             | 173              |
| <i>Ocnerodrilus</i> sp. 4  | Endogeic     |                       |                            | 50              |                  |
| <i>Ocnerodrilus</i> sp. 5  | Endogeic     |                       |                            | 276             |                  |
| <i>Ocnerodrilus</i> sp. 6  | Endogeic     |                       |                            | 32              |                  |
| Rhinodrilidae family       |              |                       |                            |                 |                  |
| <i>Andiorrhinus</i> sp. 1  | Epi-endogeic |                       |                            |                 | 7                |
| <i>Andiorrhinus</i> sp. 2  | Epi-endogeic |                       |                            | 133             |                  |
| <i>Andiorrhinus</i> sp. 3  | Endo-anecic  |                       |                            |                 | 460              |
| <i>Andiorrhinus</i> sp. 4  | Endo-anecic  |                       |                            |                 | 10               |
| <i>Andiorrhinus</i> sp. 5  | Endo-anecic  |                       |                            |                 | 70               |
| <i>Andiorrhinus</i> sp. 6  | Endo-anecic  |                       |                            | 175             |                  |
| <i>Andiorrhinus</i> sp. 7  | Endo-anecic  |                       | 11                         |                 | 129              |
| <i>Andiorrhinus</i> sp. 8  | Endo-anecic  |                       | 23                         |                 |                  |
| <i>Andiorrhinus</i> sp. 9  | Endo-anecic  |                       | 139                        |                 |                  |
| <i>Andiorrhinus</i> sp. 10 | Endo-anecic  |                       | 471                        | 220             |                  |
| <i>Andiorrhinus</i> sp. 11 | Endo-anecic  |                       | 489                        |                 |                  |
| <i>Andiorrhinus</i> sp. 12 | Endo-anecic  |                       | 6                          |                 |                  |
| <i>Andiorrhinus</i> sp. 13 | Epi-endogeic |                       |                            | 47              |                  |
| <i>Andiorrhinus</i> sp. 14 | Epi-endogeic |                       |                            | 44              |                  |
| <i>Andiorrhinus</i> sp. 15 | Epi-endogeic |                       |                            |                 | 31               |

| Earthworm taxonomy             | Ecotype      | Biogeographic regions |                            |                 |                  |
|--------------------------------|--------------|-----------------------|----------------------------|-----------------|------------------|
|                                |              | Low Coastal Plain     | Hilly Sand and Clay Region | Highland Region | Interior Savanna |
| <i>Andiorrhinus</i> sp. 16     | Epi-endogeic |                       |                            | 159             |                  |
| <i>Aptodrilus</i> sp.          | Epi-endogeic |                       |                            |                 | 9                |
| <i>Estherella</i> sp. 1        | Epigeic      |                       |                            | 36              | 49               |
| <i>Estherella</i> sp. 2        | Endogeic     |                       |                            | 81              |                  |
| <i>Periscolex</i> sp.          | Endogeic     | 1606                  | 196                        | 307             |                  |
| <i>Pontoscolex corethrurus</i> | Endogeic     | 109                   | 827                        | 990             | 581              |
| <i>Pontoscolex</i> sp. 1       | Endogeic     |                       | 219                        | 283             |                  |
| <i>Pontoscolex</i> sp. 2       | Endogeic     |                       | 185                        |                 |                  |
| <i>Pontoscolex</i> sp. 3       | Endogeic     |                       |                            | 633             |                  |
| <i>Rhinodrilus</i> sp. 1       | Anecic       |                       |                            | 35              | 9                |
| <i>Rhinodrilus</i> sp. 2       | Endogeic     | 24                    |                            |                 |                  |
| <i>Rhinodrilus</i> sp. 3       | Epi-endogeic |                       |                            | 160             |                  |
| <i>Rhinodrilus</i> sp. 4       | Epi-endogeic |                       | 138                        | 20              |                  |
| <i>Rhinodrilus</i> sp. 5       | Epi-endogeic |                       | 148                        |                 |                  |
| <i>Rhinodrilus</i> sp. 6       | Anecic       |                       |                            | 269             | 160              |
| <i>Thamnodrilus</i> sp. 1      | Epigeic      |                       |                            | 3               |                  |
| <i>Thamnodrilus</i> sp. 2      | Epigeic      |                       |                            | 401             |                  |
| <i>Urobenus</i> sp.            | Epi-endogeic | 7                     |                            |                 |                  |
| Total abundance                |              | 6437                  | 5232                       | 7291            | 3075             |
| Total richness (S)             |              | 16                    | 23                         | 34              | 19               |

families – Benhamiidae (3 msp.), Almiidae (3 msp.), Megascolecidae (2 msp.), Acanthodrilidae (1 msp.) and Eudrilidae (1 msp.) – accounted for a minority of the identified taxa.

*Pontoscolex corethrurus* (Müller, 1857) was the most dominant species, accounting for nearly 12 % of the total individuals sampled. Dominance, however, was different across biogeographical regions. *Periscolex* sp. was the most abundant in the Low Coastal Plain (25 %), while *Dichogaster* sp. 1 accounted for 20.5 % of the Hilly Sand and Clay Region, *Dichogaster* sp. 2 accounted for 17 % in the Highland Region, and *P. corethrurus* accounted for 19 % of the abundance in the Interior Savanna.

The highest Hill-Shannon diversity ( $q = 1$ ) and species richness ( $q = 0$ ) were recorded in the Highland Region (20, 34 species), followed by the Hilly Sand and Clay Region (13, 23 species), Interior Savanna (11, 19 species) and Low Coastal Plain (9, 16 species), (Fig. 2).

### Abundance and ecotype distribution across biogeographic regions

Geography had a statistically significant impact on earthworm abundance ( $p = 0.008$ ) and species richness ( $p = 0.034$ ). The Highland Region had the highest estimated mean abundance and species richness, while the Interior Savanna had the lowest estimated abundance and the

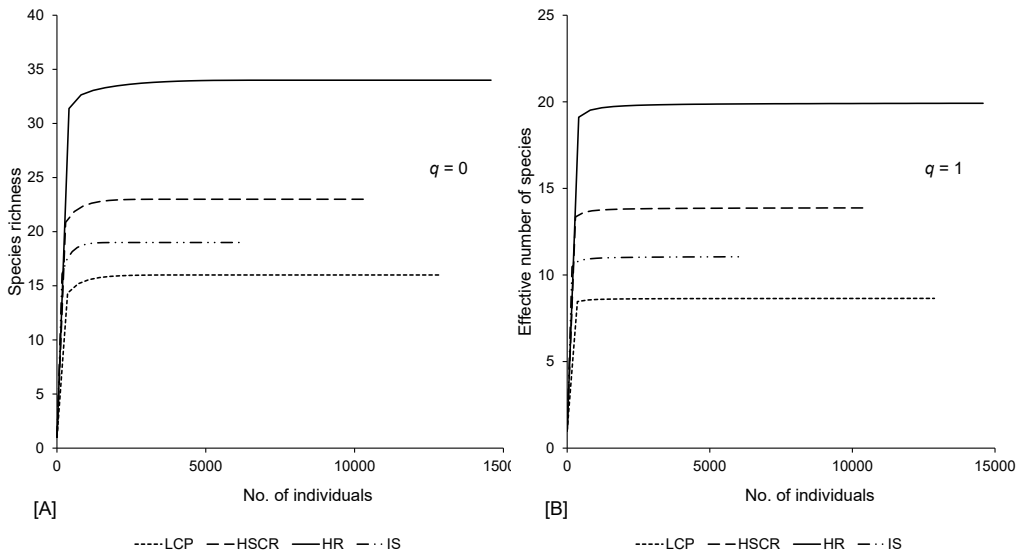


**Fig. 2. Regional comparison of rarefaction curves for earthworms within Low Coastal Plain (LCP), Hilly Sand and Clay Region (HSCR), Highland Region (HR), Interior Savanna (IS).**

Note:  $q = 0$  represents species richness and  $q = 1$  represents the Hill-Shannon diversity.

Low Coastal Plain with the lowest estimated species richness (Fig. 3). Earthworm abundance in the Highland Region and Low Coastal Plain was significantly different than that of the Interior Savanna.

### Relationships with soil types and their attributes

Earthworm abundance ( $p = 0.04$ ) and species richness ( $p = 0.026$ ) varied significantly across the soil types. Among the 11 types analysed, Anthrosols were associated with the highest mean abundance (Fig. 4). In the Anthrosols, the hortic Anthrosol supported the highest mean abundance and species richness, while hydagic Anthrosols were associated with the lowest. On the opposite end of the spectrum, Leptosols supported the overall lowest av-

erage abundance when compared to the other soil types. Earthworm abundances in terric Anthrosols and Acrisols were the most significantly different while species richness in Leptosols, terric Anthrosols and hydagic Anthrosols were significantly different from hortic Anthrosols.

The marginal PERMANOVA analysis revealed that earthworm ecotype community composition was significantly structured by calcium ( $p = 0.006$ ,  $R^2 = 0.07$ ), phosphorus ( $p = 0.006$ ,  $R^2 = 0.06$ ) and iron ( $p = 0.016$ ,  $R^2 = 0.05$ ). These three edaphic variables alone were responsible for almost 19 % of the observed variation. Further analysis revealed that anecic abundance increased with phosphorus while the inverse was observed for endo-anecic abundances with iron and calcium (Table 2).

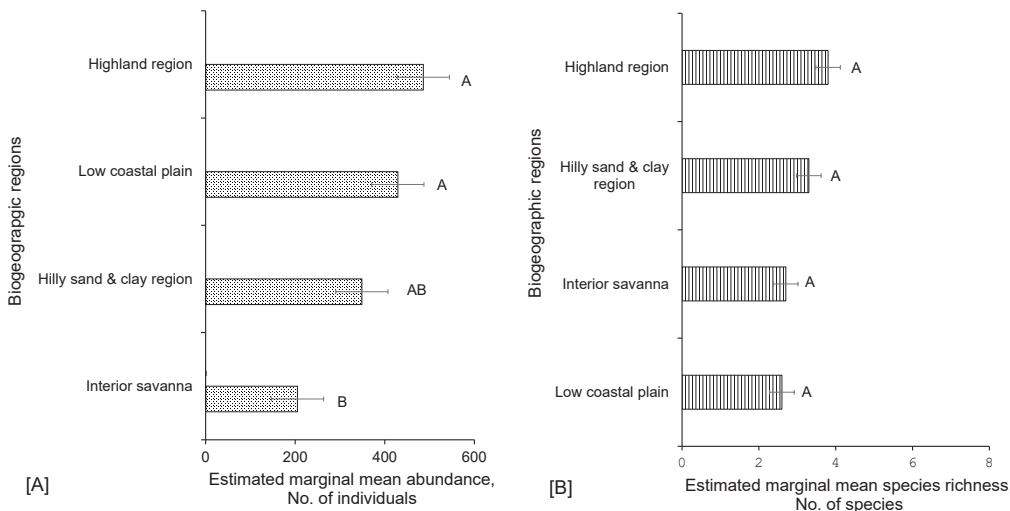


**Fig 3. Regional comparison of earthworms across the biogeographic regions [A] Estimated marginal mean abundance [B] Estimated marginal mean species richness of earthworms**

Note: Uppercase letters indicate statistically significant pair-wise differences between biogeographic regions.

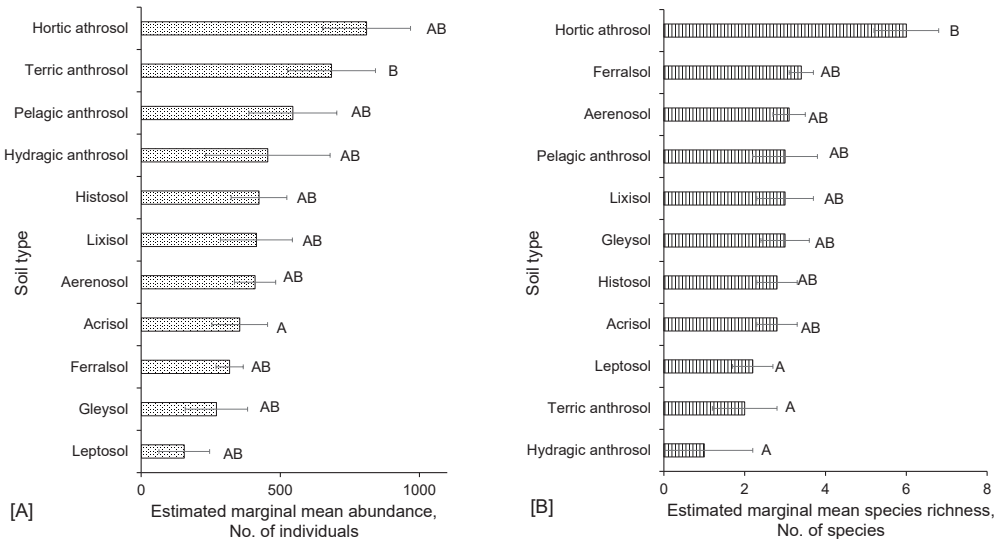


**Fig 4. Comparison of earthworm [A] Estimated marginal mean abundance [B] Estimated marginal mean species richness across different soil types.**

Note: Uppercase letters indicate statistically significant pair-wise differences between soil types.

**Table 2. Directional coefficients from an mGLM between ecotype abundance and significant edaphic variables.**

| Ecotype                | Phosphorus   | Calcium       | Iron          |
|------------------------|--------------|---------------|---------------|
| Epigeic abundance      | 0.006        | -0.187        | -0.236        |
| Epi-endogeic abundance | 0.375        | 0.743         | -0.347        |
| Endogeic abundance     | -0.153       | -0.032        | 0.340         |
| Endo-anecic abundance  | 0.080        | <b>-1.578</b> | <b>-1.851</b> |
| Anecic abundance       | <b>1.030</b> | <b>-1.110</b> | 0.057         |

Note: Bold values indicate significant directional coefficients.

### Effect of habitat, disturbance and climate

Both abundance ( $p = 0.056$ ) and species richness ( $p = 0.4$ ) did not vary significantly between habitat types. Of the seven habitat types surveyed, farms had the highest mean abundance followed by grasslands and montane forests, respectively; while the highest mean species richness was associated with montane forests. The lowest mean abundance and species richness

were consistently associated with savanna habitats (Fig. 5). The abundances between farms and savanna habitats were the most significantly different.

Climate had a significant influence on both earthworm abundance ( $p < 0.001$ ) and species richness ( $p < 0.001$ ). The highest abundances and species richness were found in areas with a monsoon climate followed by equatorial and tropical savanna climates, respectively (Fig. 6).

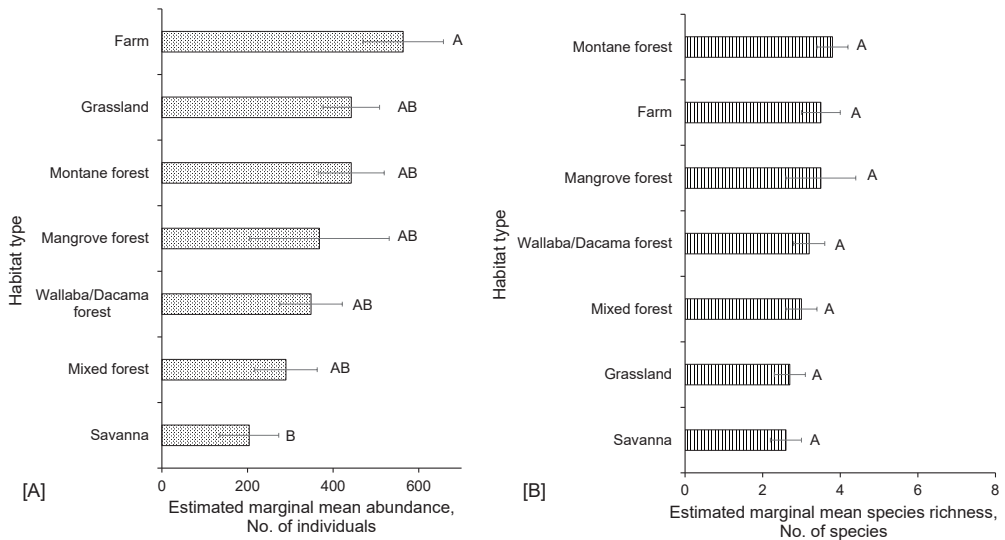


**Fig. 5. Comparison of earthworm [A] Estimated marginal mean abundance [B] Estimated marginal mean species richness across different habitat types.**

Note: Uppercase letters indicate statistically significant pair-wise differences between soil types.

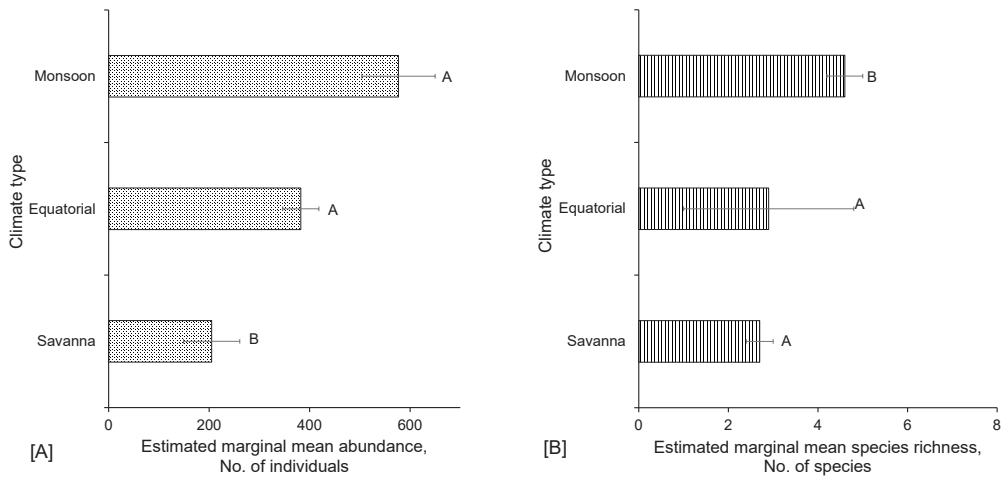


**Fig. 6. Comparison of earthworm [A] Estimated marginal mean abundance [B] Estimated marginal mean species richness across different climate types.**

Note: Uppercase letters indicate statistically significant pair-wise differences between soil types.

The abundances within monsoon and equatorial climates were significantly different from that of the savanna climate and the species richness within the monsoon climate was significantly different from equatorial and tropical savanna climates.

The study assessed 35 disturbed sites and 25 conserved sites; no significant difference was observed for both abundance ( $p = 0.84$ ) and species richness ( $p = 0.44$ ).

### Community composition

Multivariate analysis confirmed that earthworm ecotype composition was significantly structured by environmental variables. Soil type (PERMANOVA:  $R^2 = 0.39$ ,  $p < 0.001$ ), habitat type (PERMANOVA:  $R^2 = 0.19$ ,  $p = 0.011$ ) and biogeographic region (PERMANOVA:  $R^2 = 0.16$ ,  $p < 0.001$ ) were the strongest predictors of community composition, while disturbance (PERMANOVA:  $R^2 = 0.08$ ,  $p < 0.001$ ) and climate type (PERMANOVA:  $R^2 = 0.07$ ,  $p =$

0.03) also exerted significant but less pronounced influences.

Further *post-hoc* GLM analysis revealed how ecotype abundance was structured within each region (Fig. 7).

While endogeic earthworms were the most abundant of the ecotypes across the biogeographical regions, there was no significant difference between their estimated mean abundance (Fig. 8). In contrast, endo-anecic and anecic ones were the least abundant within the Low Coastal Plain and Hilly Sand and Clay Region respectively, while epi-endogeic earthworms were the least abundant in the Highland Region and the Interior Savanna.

NMDS ordination (Fig. 9) further illustrated the relationship between soil types and ecotypes. Ferralsols and Aerenosols clustered at opposite ends of NMDS2 axis, illustrating a shift from endogeic dominance to epigeic dominance in the latter soil type. Epi-endogeic earthworms were mostly restricted to terric Anthrosols and Gleysols, as indicated by their posi-

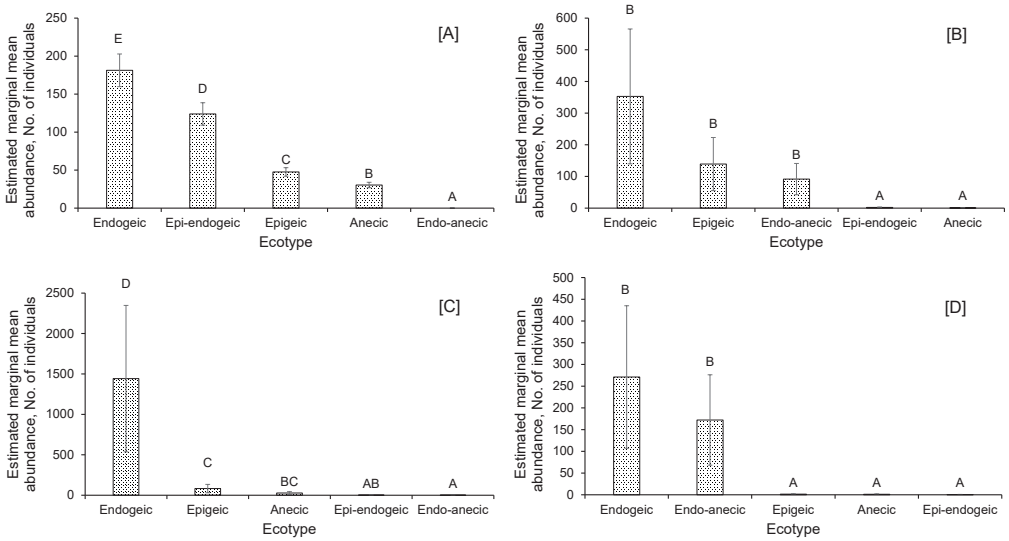


**Fig. 7. Estimated marginal mean abundance of earthworm ecotypes in the [A] Low Coastal Plain, [B] Hilly Sand and Clay Region, [C] Highland Region, and [D] Interior Savanna, as predicted by negative binomial GLMs.**

Note: Uppercase letters (A–E) indicate significance ( $p < 0.05$ , Tukey adjusted).

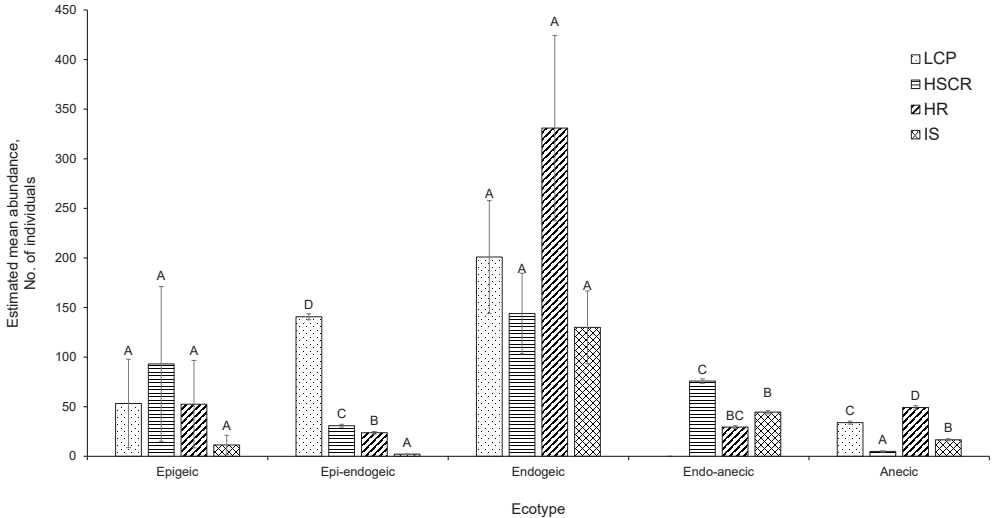


**Fig. 8. Comparison of the estimated marginal mean abundance of earthworm ecotypes among the Low Coastal Plain (LCP), Hilly Sand and Clay Region (HSCR), Highland Region (HR), and Interior Savanna (IS), as predicted by negative binomial GLMs.**

Note: Uppercase letters (A–D) indicate significance ( $p < 0.05$ , Tukey adjusted).

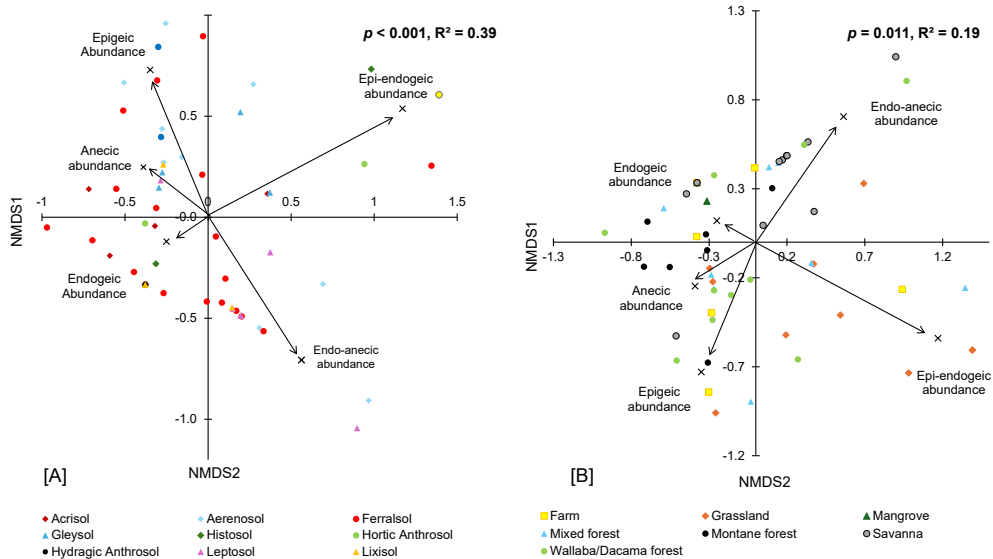


**Fig. 9. NMDS ordination showing differences in earthworm ecotype composition among [A] soil types and [B] habitat types.**

tioning along NMDS1 axis. Wallaba/Dacama forests and montane forests formed distinct clusters along NMDS2 axis showing a transition from epigeic dominance to anecic while endo-anecic earthworms dominated the savannas.

## Discussion

### Drivers of species dominance

The high abundance of *P. corethrurus* observed in this study is likely a function of this species' high ecological plasticity. This species is known to effectively out-compete native taxa by exploiting new niches created by disturbance, allowing it to thrive in a variety of anthropogenic ecosystems (Lapied and Lavelle 2003, Marichal et al. 2010). Similarly, the dominance of *Dichogaster* sp. 1 and *Dichogaster* sp. 2 in the Hilly Sand and Clay Region

and Highland Region suggests successful colonisation by these invasive taxa, likely facilitated by human-induced introduction and anthrope-pedological pressures in these areas. This genus contains numerous invasive species that exploit available niches and can become dominant. They have been documented in neighbouring Brazil (Brown et al. 2006, Mota et al. 2025), and throughout much of Latin America (Fragoso and Brown 2007).

### Biogeographical influence

The Highland Region supported the highest earthworm abundance, likely due to its diverse tropical forests. These ecosystems provide abundant food sources in the form of detritus and root exudation, as well as diverse niches, which, when coupled with high precipitation and stable warm temperatures, create an optimal environment for biomass accumulation (Fit-

tkau and Klinge 1973, Brown 2013).

The variation in ecotype abundance across the biogeographical regions can also be attributed to diverging reproductive strategies. Epigeic species are typically R-strategists, characterised by smaller bodies and high fecundity rates, which allow for rapid population growth in the nutrient-rich soil surface layer (Domínguez 2018). In contrast, most anecic species are generally K-strategists, with larger bodies and lower fecundity rates (Cosin et al. 2011). The proliferation of endogeic species in all regions, particularly the Highland Region, could be attributed to their selective geophagous feeding habits and their resilience which makes them less sensitive to variables that would otherwise disrupt other ecotypes (Lavelle and Spain 2001, Lwanga et al. 2023).

The low abundance of anecic species in the Hilly Sand and Clay Region may be a result of higher anthropogenic disturbance in this region limiting resource availability and intensifying competition between epigeic and anecic species due to their niche overlap (Palm et al. 2012). The lower abundance observed in the Interior Savanna may also be a result of environmental stressors such as dry spells and higher temperatures, characteristic of tropical savanna ecosystems (Bohlen 2002, Pennington et al. 2018).

### Edaphic influence

Soil type was an important determinant of earthworm community structure. Hortic Anthrosols (black earth) exhibited the highest relative abundance, which can be attributed to their high fertility and loose structure, due to centuries' worth of practices of adding organic waste and charcoal to the soil (Sombroek 1966). This nutrient-rich edaphic environment supports

high earthworm abundances that facilitate niche overlap while reducing competition. Similar results have been observed elsewhere, in several Brazilian Amazonian sites with dark earth soils (Demetrio et al. 2021).

Hydragric Anthrosols (lowest species richness) are water-saturated soils that create a hypoxic environment (Bohlen et al. 2004), making them almost uninhabitable for soil dwelling species. This environment effectively limits the assemblage to surface-dwelling epigeic species. Similarly, the low abundances observed in Leptosols are likely due to their high sand content and susceptibility to waterlogging. These properties cause mechanical abrasion, drowning and physiological stress, leading to higher mortality rates and lower earthworm abundances (Edwards 2004, Chauhan 2014).

Earthworm abundance was strongly influenced by soil phosphorus (P), iron (Fe) and calcium (Ca). The relationship between P dynamics and earthworm activity is a highly interlinked feedback-driven process. While P significantly influences the spatial distribution of earthworms (Nuutinen et al. 1998), the dynamic interactions between these organisms and the soil matrix heavily influence phosphorus concentration in the upper soil layer (Le Bayon and Milleret 2009). Litter-derived Ca plays an important role in promoting earthworm abundance (Reich et al. 2005), with higher levels of Ca being associated with metabolic efficiency in earthworms, particularly those species that are involved in organic matter decomposition. In the present case, higher soil Ca represented lower endo-anecic and anecic abundances which was observed by Frago and Lavelle (1992) for tropical rain forests around the world. Fe in the form of hematite and goethite impacts soil texture

by acting as a cementing agent; this increases penetration resistance and could limit the soil dwelling species as seen in this study (Bullinger-Weber et al. 2007, Stefanou and Papazafeiriou 2013).

### Habitat and land use dynamics

Farms exhibited the highest earthworm abundances, likely due to the specific management practices utilised and the presence of invasive species like *Dichogaster*. Several of the farms sampled did not utilise synthetic pesticides and fertilisers and, as such, the chemical integrity of the soil was not compromised, allowing earthworms to flourish within these environments. On the other hand, the mechanical overturning of soil associated with farming could have negatively impacted community structure. Tillage forces geophagous species to the surface while burying epigeic species, the latter of which are generally unaffected (Edwards and Arancon 2022).

In contrast, the savanna habitats of Guyana appear to be significantly more stressful environments than the rainforests. The savannas areas have higher temperatures and lower soil moisture content, with high seasonal variability which create a stressful environment for earthworms (Kalu et al. 2015). Additionally, the higher sand content of these soils may also be suppressing earthworm abundances (Edwards 2004) in the present study. Conversely, positive relationships between earthworm abundances and sand contents were observed by López-Hernández (2012) in Venezuelan tropical savannas.

### Climatic constraints

The monsoon climate supported the highest relative abundance of earthworms by providing optimal conditions such as higher precipitation and moderate temperatures (Fragoso and Lavelle 1992). In contrast, the tropical savanna climate, characterised by lower precipitation and higher temperatures, creates physiological constraints. These conditions disrupt the earthworm's ability to regulate moisture through its skin, forcing migration into deeper soil layers, triggering diapause or leading to mortality (Chauhan 2014). These results confirm the low earthworm abundances also observed by López-Hernández (2012) in savannas of the Orinoco river basin in Venezuela.

### Disturbance

The primary anthropogenic drivers of environmental disturbance identified in this study were mining, logging and agriculture, and taken at a landscape scale, disturbance had significant impacts on earthworm abundances in two regions. Mining significantly alters the physicochemical properties of soil and depletes organic matter content, which can be detrimental to most earthworm species; however, some epigeic species have a degree of tolerance for these altered edaphic environments (Townsend and Hodgson 1973, Satchell and Stone 1977, Southwell and Majer 1982). Logging also exerts an intense localised pressure on earthworm populations. It disrupts the top 15–20 cm of soil, where most earthworms reside, exposing them to the surface where they

are threatened by increased predation and solar radiation (Sohrabi et al. 2021).

On the other hand, farming tended to have a positive impact on earthworm abundance, as mentioned previously.

### Drivers of ecotype composition

Earthworm ecotype composition across the biogeographical regions was heavily influenced by local environmental filters. Despite the significance of climate ( $p = 0.03$ ), the low  $R^2$  value (0.07) indicated that climate acted as a broad constraint rather than a primary driver of ecotype composition (Weiskopf et al. 2020). Habitat and soil type accounted for 58 % of the variance in ecotype abundance. Soil types vary in aeration, moisture retention, compaction and pH, all of which can either promote or restrict an earthworm's survivability and proliferation in their respective soil environments, influencing ecotype composition (Guild 1948, Ivask et al. 2006). These results confirm the importance of soil and habitat characteristics as the main drivers of earthworm communities as shown by Fragoso and Lavelle (1992), for tropical rainforest environments.

The clustering of Ferralsols with endogeic abundance on the NMDS ordination could indicate that this ecotype thrives in soils that are rich in hematite and goethite, which absorbs organic matter (Dick et al. 2005). Endogeic species like *P. corethrurus* have been observed in Brazilian Ferralsols (Brossard et al. 2012). In contrast to this, epigeic abundance was associated with the Aerenosols which are poor in soil organic carbon (Singh et al. 2015). Because this soil tends to be nutrient poor, they may limit geophagous species and favour the epigeic litter specialists.

The clustering of farms and grasslands with epigeic and epi-endogeic abundances on the NMDS ordination could indicate that these ecotypes dominate in relatively modified habitats. Habitat alteration can allow for the establishment and proliferation of invasive species like the epigeic *Dichogaster* which were found in many of these sites. Epigeics feed on decaying organic matter such as crop residues and their reproductive strategy allows them to proliferate easily in these types of environments (Kamboj et al. 2021).

The distinct separation of savanna habitats associated with endo-anecic abundance could indicate that these species have a competitive advantage due to their deep-burrowing nature, which protects them from the suboptimal environmental conditions that limit epigeic species (Chauhan 2014, Kalu et al. 2015), and their diverse feeding preferences. Endo-anecic species were also associated with savanna and pastures in the Venezuelan savannas (López-Hernández et al. 2014).

### Limitations and future research recommendations

Several factors may have influenced the observed population structure. Species identification relied on morphology and physiology, which could have created a skewed estimation of species richness, with the possibility of some morphotypes being classified as separate species when they were the same. Cryptic species are common in the tropics (Silva et al. 2017), and future research should incorporate molecular techniques to assess the true phylogenetic diversity of Guyana's earthworms more accurately. Additionally, targeted studies in post-mining areas could provide valuable information on the resil-

ience of earthworm species in altered environments.

## Conclusions

This study provides a comprehensive baseline of earthworm assemblages across the diverse landscapes of Guyana, identifying 68 morpho-species from 8 families and revealing clear spatial patterns in diversity, abundance and community composition. Earthworm assemblage structure varied significantly among biogeographical regions, with the Highland Region supporting the highest diversity, richness and abundance, likely driven by favourable climatic conditions and high soil organic matter.

Hypothesis (1) was supported, with observed differences in abundance and diversity among biogeographical regions. While species specific trends were not assessed, clear variations in ecotype abundance and distribution among these regions were observed. Hypothesis (2) was supported, with biogeographical, climatic and edaphic factors significantly influencing earthworm abundance. Hypothesis (3) was also supported, as significant correlations were identified between soil physicochemical properties and earthworm abundance.

Biogeographical, climatic and edaphic factors were identified as key drivers shaping earthworm abundance, diversity and ecotype distribution. Epigeic, epi-endogeic, endogeic, endo-anecic and anecic groups exhibited distinct responses to environmental gradients, reflecting differences in ecological strategies and resource use. Soil physicochemical properties, particularly phosphorus, calcium and iron, played a significant role in structuring earthworm communities. Soil type and habitat type were the most significant lo-

cal drivers that shaped the ecotype composition of earthworm communities.

Anthropogenic disturbance further influenced assemblage patterns, favouring tolerant and invasive taxa such as *P. corethrurus*, while potentially limiting more specialised species. These findings highlight the importance of integrating edaphic and climatic variables into soil biodiversity conservation and land management strategies, particularly in tropical ecosystems such as the Guiana Shield.

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## Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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## Appendix A

**Table A1. GPS coordinates (WGS 84-EPSSG: 4326) of the sample sites, in each biogeographical region.**

| Site                       | Latitude, ° | Longitude, ° | Site                        | Latitude, ° | Longitude, ° |
|----------------------------|-------------|--------------|-----------------------------|-------------|--------------|
| Low Coastal Plain          |             |              | Highland Region             |             |              |
| No 3 Village               | 6.3091312   | -57.5532646  | Potareng                    | 6.114130    | -60.090220   |
| Parika backdam             | 6.8257716   | -58.4156085  | Eping                       | 6.212231    | -60.163917   |
| Parika vegetable farm      | 6.8064630   | -58.3835574  | Wildcow                     | 6.197986    | -60.230347   |
| Fairfield                  | 6.6365669   | -57.8534752  | R7S5                        | 6.253068    | -60.141484   |
| Belfield                   | 6.7150707   | -57.9654520  | Mazaruni River-bank         | 6.222047    | -60.147767   |
| Berbice riverbank          | 6.1743416   | -57.5643692  | ATTA                        | 4.249512    | -58.843315   |
| Rose Hall                  | 6.2432307   | -57.3393605  | Turtle Mt.                  | 4.726067    | -58.742267   |
| Corriverton                | 5.9241456   | -57.1511542  | Region 8 logging concession | 4.265741    | -58.969547   |
| Nismes                     | 6.7481441   | -58.2370864  | R10S5-1                     | 4.801084    | -58.659632   |
| R5S2                       | 6.6029385   | -57.9453204  | Surama                      | 4.062393    | -59.120318   |
| Essequibo Rice-field       | 7.2432418   | -58.8104524  | FairView                    | 4.530176    | -58.726053   |
| Wakapau                    | 7.3925705   | -58.5719819  | 4 mile                      | 7.694949    | -59.944195   |
| Charity                    | 7.3925705   | -58.5719819  | R1 Forest                   | 7.766097    | -59.918543   |
| Diamond                    | 6.6987816   | -58.1720690  | R1 Grassland                | 7.710737    | -59.907527   |
| Industry                   | 6.8171800   | -58.1063750  | R1 Upland forest            | 7.740258    | -59.873231   |
| Hilly Sand and Clay Region |             |              | Interior Savanna            |             |              |
| R4S4                       | 6.3398765   | -58.2446666  | Sandcreek                   | 3.010930    | -59.520591   |
| Tapakuma creek             | 7.1860072   | -58.6055005  | Kanuku Mt.                  | 3.071560    | -59.642202   |
| Tapakuma Forest            | 7.2550057   | -58.5713661  | Yakarinta                   | 3.921045    | -59.229780   |
| Bendroff                   | 6.6457558   | -58.5491722  | Manari                      | 3.435903    | -59.774361   |
| Rockstone                  | 6.0603855   | -58.4959548  | Parickwarunau               | 3.161842    | -59.854795   |
| Bamia                      | 6.1661266   | -58.2233934  | Moco Moco                   | 3.333957    | -59.650656   |
| Ituni                      | 5.5856040   | -58.2134464  | Yupukari                    | 3.659509    | -59.335163   |
| Kwakwani                   | 5.2453332   | -58.0400003  | Nappi                       | 3.398823    | -59.547154   |
| Frenchman                  | 5.1185482   | -58.7268608  | Marudi                      | 2.362333    | -59.202192   |
| Siparuta                   | 5.2296891   | -57.3033333  | Dadanawa                    | 2.819184    | -59.510550   |
| Orealla Lowland Forest     | 5.2155911   | -57.3496329  | Aishalton                   | 2.485087    | -59.293328   |
| Orealla bank               | 5.3982434   | -57.4050253  | Moreiru                     | 3.912197    | -59.488491   |
| Orealla upland forest      | 5.3307295   | -57.3600724  | Karasabai                   | 4.058325    | -59.543540   |
| Mabura                     | 5.4147070   | -58.5519211  | Schulinab                   | 3.0590547   | -59.779025   |
| Capoey Lake                | 7.1796600   | -58.5270909  | Akanukumt                   | 2.9761752   | -59.603332   |