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Does Seasonality Influence the α and β-diversity of Soil Fauna? A Case Study of Terrestrial Isopods (Isopoda, Oniscidea) Assemblage in the Colombian Caribbean Tropical Dry Forest

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Terrestrial isopods are important to forest soils, breaking down decaying plant material and aiding in nutrient recycling. Despite their ecological significance, studies on their diversity and dynamics in Neotropical dry forests are limited. This research investigated the seasonality of the alpha and beta diversity of terrestrial isopod assemblages in a protected fragment of Tropical Dry Forest in the Colombian Caribbean. We sampled isopods in 1 m^2 units of litter, and recorded soil and litter temperatures, and moisture during twelve field trips conducted between June 2018 and March 2019 in rainy, transition, and dry climatic seasons. A total of 867 individuals belonging to four families, six genera, and eight species were collected. Alpha diversity did not show significant differences across seasons. However, abundance was significantly influenced by seasonality, soil temperature, litter temperature, and soil moisture. Moreover, species richness was affected by soil moisture and litter temperature. Our results highlight pronounced seasonality in the isopod assemblage, characterized by balanced variation in beta diversity, with higher abundance during the transition and rainy seasons. The observed increase in the variables, correlated with higher total beta diversity, underscores their role as drivers of seasonal dynamics in assemblage structure. Soil temperature and moisture significantly influenced balanced variation component of beta diversity. The identified seasonal pattern likely results from the historical adaptive processes of these species to the conditions of the tropical dry forest. Nonetheless, effective conservation strategies are essential to mitigate the impacts of climate change on edaphic arthropod assemblages in this ecosystem.

Key words: Seasonal diversity, Neotropical, Climate change, Woodlice, Soil arthropods

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BACKGROUND

Colombia has been identified as one of the most vulnerable countries to climate change impacts such as higher temperature, increased average precipitation, and changes in El Niño and La Niña events. The Colombian Caribbean could be particularly affected (Rodríguez 2013). This region exhibits marked seasonality, characterized by a bimodal regime with a pronounced dry season at the beginning of the year followed by a rainy season with abundant precipitation (Rangel-Ch and Carvajal-Cogollo 2012; Guzmán et al. 2014). Global climate models predict changes in precipitation patterns and an increase in the frequency and severity of droughts by the end of this century (IPCC 2014 2018). These changes are likely to affect the structure and function of ecosystems, particularly in areas where water availability is the main limiting factor for soil organisms. The goal of this study is to evaluate the effect of seasonality on the alpha and beta diversity of terrestrial isopod assemblages in the Colombian Caribbean Tropical Dry Forest (TDF), to better understand how these organisms respond to environmental variations.

Soil fauna comprises invertebrates that either permanently reside in soil or undergo one or more development stages in it (De Aquino and Correira 2005; Kern and Köhler 2012). Terrestrial isopods, commonly known as "woodlice", are integral to soil fauna and are recognized as important detritivores in numerous Neotropical forests and habitats (Leistikow 2001). They play a key role in decomposing and dispersing soil organic matter (Kern and Köhler 2012; Ŝpaldoňová and Frouz 2014; Abd El-Wakeil 2015), breaking down the litter layer which provides the main biodegradable organic material (Webb 1977; Förster et al. 2006; Quadros and Araujo 2008). They can also be used as bioindicators of environmental and anthropogenic impacts (Dallinger et al. 1992; Paoletti and Hassall 1999) and as research model organisms (Zimmer and Topp 1999; Araujo and Bond-Buckup 2005; Lesĕr et al. 2008; Ŝpaldoňová and Frouz 2014). They exhibit unique characteristics in ecophysiology and reproduction strategies, making them valuable for studying the effects of environment alterations and climate change (Sfenthourakis and Hornung 2018; Brigić et al. 2019; Antoł et al. 2021). Terrestrial isopods belong to the Oniscidea suborder, the sole Isopoda group fully adapted to terrestrial environments (Taiti 2018; Sfenthourakis et al. 2020). It encompasses around 4,000 species distributed across all global regions except the poles (Schmalfuss 2003; Sfenthourakis and Taiti 2015; Campos-Filho and Taiti 2021). They have been recorded from marshy to desert areas, and from coastal regions to high mountains, always looking for refuges to protect themselves from dehydration (Schmalfuss 2003; Campos-Filho et al. 2018; López-Orozco et al. 2022; Ocampo-Maceda et al. 2022).

Oniscidean isopods exhibit high sensitivity to variations in different abiotic factors. Environmental variables such as temperature and precipitation play essential roles in the dynamics of these assemblages as they modify their growth, survival, and reproduction (Waller and Verdi 2018). Similarly, humidity and ground-level radiation can cause changes in species richness and abundance (Zimmer 2005; Kern and Köhler 2012; Solomou et al. 2019). Several studies indicate a close association between the richness and abundance of terrestrial isopods and fluctuations in soil temperature and humidity (Araujo and Bond-Buckup 2005; Quadros and Araujo 2007; Fingini 2008; Kern and Köhler 2012; Waller 2012). Only one ecological study has been conducted in Colombia (Preciado and Martínez 2014). In it, the authors found no direct relationship between environmental variables such as soil and ambient temperature, relative humidity, and the richness and abundance of isopods. However, they suggest that soil conditions or characteristics, including humidity, water table, and composition, may be more decisive in determining the number of Oniscids found in a given habitat.

The TDF is recognized as strategic biome of low-lying areas, exhibiting a high degree of endemism within the Neotropical region (Olson et al. 2001; Lamoreux et al. 2006; Pennington et al. 2006; Morrone 2014; Banda-R et al. 2016). This ecosystem spans elevations between 0-1,000 m a.s.l., with some areas reaching heights of up to 2,200 m (Trejo-Vázquez 1999; Miles et al. 2006). It is characterized by distinct climatic seasons marked with a very long period of drought with high temperatures, followed by rainy seasons for short periods, which strongly influence the life forms inhabiting this environment (Murphy and Lugo 1986; IAVH 1997, 1998). Consequently, organisms in this biome must develop various adaptations to survive in these extreme conditions. During the dry period, vegetation cover typically sheds foliage as a strategy to avoid desiccation and conserve energy (Murphy and Lugo 1986; IAVH 1998). The Colombian Caribbean hosts fragments of TDF that are among the best conserved in the country. However, this ecosystem is currently facing an alarming level of threat globally due to multiple factors, primarily associated with agricultural activities that have led to its fragmentation and decline.

The study aimed to examine the impact of seasonal changes on the diversity of terrestrial isopod communities in the Colombian Caribbean TDF. Specifically, it focused on assessing the alpha and beta diversity of these assemblages to provide insight into their resilience and adaptability to environmental fluctuations. By advancing our understanding of isopod responses to seasonal shifts, this study contributes to broader knowledge of biodiversity dynamics within a threatened and ecologically valuable biome. Given that only 5% of Colombia's TDF is protected under the National System of Protected Areas, this research also underscores the need for enhanced conservation efforts (Janzen 1988; Etter 1993; García et al. 2014).

MATERIALS AND METHODS

Study area

The Botanical Garden of Cartagena "Guillermo Piñeres" (BGGP) is located in the Matute sector of the municipality of Turbaco, Bolívar department (Colombian Caribbean), at the geographical coordinates 10°21'16.35"N and 75°25'40.27"W (Fig. 1). The weather in this area is influenced by the movements of the Intertropical Convergence Zone (ITCZ) and three climatic seasons are recognized: 1. Dry (December-April), characterized by strong winds and low precipitation; 2. Transition (May-August), in which rains and dry periods occur; and 3. Rainy (September-November), marked by increased rainfall. The duration and intensity of these seasons may vary due to the influence of the American Monsoon System, low-level atmospheric wind currents, and El Niño and La Niña events (Angulo 1974; CIOH 2007; Rangel-Ch and Carvajal-Cogollo 2012; Sierra-Labastidas et al. 2014).

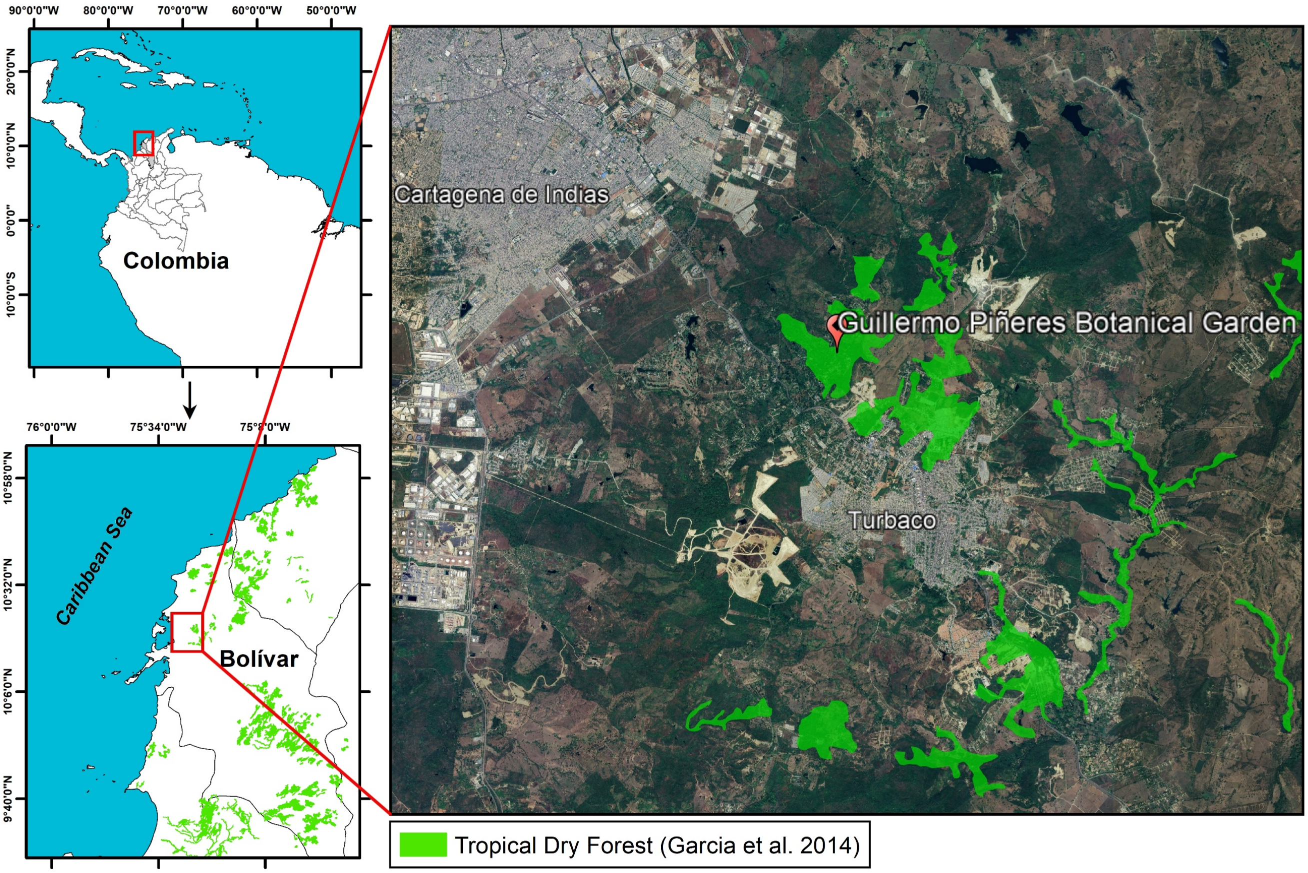

Fig. 1. Location of the Botanical Garden of Cartagena "Guillermo Piñeres" in the north of Bolívar, Colombian Caribbean. Green area: Colombian Tropical Dry Forest (Garcia et al. 2014).

The BGGP is situated at an altitude of 130 m and presents an average annual temperature of 28°C, annual rainfall ranges between 900 and 1,200 mm, with an average relative humidity of 70% (Londoño-Lemos et al. 2022). The site features springs originating on the property, primarily from the Matute stream. It represents one of the preserved TDF fragments in the Colombian Caribbean, and is considered a Key Biodiversity Area (KBA) a global level (Garcia et al. 2014; Londoño-Lemos et al. 2022; Key Biodiversity Areas Partnership 2024). The BGGP encompasses nine hectares, including a patch of Native Forest, live plant collections (Arboretum, Palmetum, Fruit trees, and Ornamentals), and several habitats such as moss and fern gardens (Londoño-Lemos et al. 2022; JBGP 2024). The Arboretum collection and Native Forest were selected as the samples areas for terrestrial isopods. Native Forest (Fig. S1) can be considered a gallery forest, characterized by abundant vines, woody climbers, and trees exceeding 10 meters in height with well-developed crowns, being representative *Brosimum alicastrum* Sw., *Trophis racemosa* (L.) Urb., *Morisonia frondosa* (Jacq.) Christenh. & Byng, *Anacardium excelsum* (Kunth) Skeels, *Guarea guidonia* (L.) Sleumer, *Sterculia apetala* (Jacq.) H.Karst., and *Swietenia macrophylla* King. (Londoño-Lemos et al. 2022). The Arboretum collection (Fig. S2) consists primarily of timber tree species of economic interest and/or endangered status, such as *Cedrela odorata* L. 1753 and *Leuenbergeria guamacho* (F.A.C.Weber) Lodé, as well as common fruit trees in the region, like *Mammea americana* L. 1791.

Sampling and taxonomic identification

The samples was conducted during specific climatic season between 08:00 and 17:00 hours in June-July 2018 (Transition season), October-November of the same year (Rainy season), and February-March 2019 (Dry season). Twelve samples were carried out, six were conducted in each sample area, and four were conducted per season. The sampling method described by Sokolowicz (2010) was adopted for specimen collection. This involved using an 18 m long by 6 m wide transect divided into seven quadrats of 3 × 3 m within both the Native Forest and Arboretum. Within each quadrat, a sample unit measuring 1 × 1 m was randomly selected using a dice; the first throw determined the number of meters forward, and the second throw indicated the number of meters sideways. Litter covering a 1 m^2 area was sieved using a Winkler sifter with a 30 cm diameter and a 1 cm mesh size. The sieved material was then spread onto a white cloth, and specimens were picked out using soft tweezers and deposited into 15 mL plastic bottles containing 70% ethanol. To study the relationship between soil/litter (decaying leaves bed) temperature and the structure of the isopod assemblage, soil temperature was measured using a soil thermometer in each quadrant. Soil moisture was assessed by collecting samples from intercalated quadrants, which were then weighed. After 72 hours at 100°C, the dry weight was obtained, and the difference in weights was divided by the dry weight and multiplied by 100 to calculate the soil moisture percentage.

The collected individuals were identified using morphological characters, following López-Orozco et al. (2016), Carpio-Díaz et al. (2018 2023), and Campos-Filho et al. (2020). Specimens were preserved in 75% ethanol and stored in the Laboratory of the Hydrobiology Research Group within the Biology Program at the University of Cartagena.

Data analysis

All analyses were performed using RStudio v4.2.0 (R Core Team 2020). Alpha and beta diversity graphics were generated using the "ggplot2" package (Wickham 2016).

α-diversity

We assessed the completeness of sampling by applying Chao et al. (2014) method, using extrapolation-interpolation curves to estimate sample coverage based on abundance data, following the methodologies proposed by Chao et al. (2014) and Colwell et al. (2012). To characterize terrestrial isopods assemblage alpha diversity, we use effective species numbers for each climatic season, representing three diversity orders: *q*0 (number of observed species), *q*1 (exponential of the Shannon index), and *q*2 (inverse of the Simpson index) (Hill 1973; Moreno et al. 2011; Chao et al. 2016). We calculated 95% confidence intervals for each *q* order using 500 bootstrap pseudoreplicates and constructed alpha diversity profiles. These analyses were performed using "iNEXT" package and the online iNEXT tool (Chao et al. 2016; Hsieh et al. 2016). Additionally, to compare richness, abundance, and uniformity patterns across seasons, rank/abundance curves were generated using Log_{10} transformed abundance data, following Whittaker's (1972) approach.

Generalized Linear Models (GLMs) were performed to assess the effect of litter temperature, soil temperature, soil moisture, and seasonality on abundance and diversity orders. Abundance was fitted to a Poisson distribution, while diversity orders (*q*0, *q*1, *q*2) followed a normal distribution. The best-fitting models were selected based on the Akaike Information Criterion (AIC) (Akaike 1974), and an ANOVA was conducted to determine the contribution of each explanatory variable (abundance and diversity orders). These analyzes were carried out using the "glmnet" package (Friedman et al. 2010).

β-diversity

The abundance matrix was initially transformed using the fourth root method to mitigate the influence of dominant species. Subsequently, we conducted a Permutational Analysis of Variance

(PERMANOVA) of one-way using the Bray-Curtis index with 999 permutations to evaluate differences in the assemblage structure between seasons (Anderson 2001). This analysis used the *adonis2* function from "vegan" package (Oksanen et al. 2019). To assess differences between pairs of seasons, we employed the *pairwise.adonis* function from the "pairwiseAdonis" package (Martinez 2020).

Beta diversity and its components (balanced variation in abundance and abundance gradients) were assessed following Baselga's proposal (2010, 2013, 2017) by implementing the functions *beta.multi.abund* and *beta.pair.abund* with the Bray-Curtis index through the "betapart" package (Baselga 2010, 2013, 2017; Baselga and Orme 2023). Non-metric Multidimensional Scaling (NMDS) ordination was used to visualize differences identified in the PERMANOVA results. This was conducted using the "vegan" package *meta*MDS function (Oksanen et al. 2019). NMDS and PERMANOVA was performed separately for total beta diversity and each component to elucidate the modulating processes.

Finally, the Mantel test was used to evaluate the correlation between total beta diversity, its components, and soil environmental variables, examining whether observed changes in beta diversity were associated with variation in environmental factors. The Mantel test used the *mantel* function from "vegan" package, with 999 permutations (Mantel 1967; Mantel and Valand 1970; Oksanen et al. 2019).

RESULTS

Composition and abundance of the assemblage

A total of 867 individuals were collected, comprising eight species from four families and six genera of oniscideans (Table 1). The family Philosciidae Kinahan, 1857 exhibited the highest richness (three species), followed by Armadillidae Brandt, 1831 and Platyarthridae Verhoeff, 1949, each with two species. The family Scleropactidae Verhoeff, 1938 was represented by one species.

The most abundant family was Philosciidae (*n* = 611, 70.5%), followed by Platyarthridae (*n* = 102, 11.8%). Armadillidae (*n* = 84, 9.7%) and Scleropactidae (*n* = 70, 8.1%) were the families with the lowest abundance. The most abundant species were *Androdeloscia* sp., with 412 individuals, *Androdeloscia colombiana* with 189, *Trichorhina bermudezae* with 94, *Colomboniscus carpioi* with 70, and *Venezillo gigas* with 59 individuals. In comparison, *Ischioscia* sp. had ten, and *Trichorhina heterophtalma* had eight, the latter being the species with the lowest number of individuals (Table 1).

Table 1. Composition and abundance of terrestrial isopods assemblage collected during different climatic seasons at the Botanical Garden of Cartagena "Guillermo Piñeres" in the Colombian Caribbean

Family	Species	Transition season	Rainy season	Dry season	Total
Armadillidae	*Ctenorillo dazai* Carpio-Díaz, López-Orozco & Campos-Filho, 2018	18	6	1	25
	Venezillo gigas (Miers, 1878)	53	1	5	59
Philosciidae	*Androdeloscia* sp.	304	82	26	412
	Androdeloscia colombiana López-Orozco, Carpio-Díaz & Campos-Filho, 2016	106	69	14	189
	Ischioscia sp.	0	10	0	10
Platyarthridae	*Trichorhina bermudezae* Carpio-Díaz, López-Orozco & Campos-Filho, 2018	91	2	1	94
	Trichorhina heterophtalma Lemos de Castro, 1964	4	0	4	8
Scleropactidae	*Colomboniscus carpioi* Carpio-Díaz, López-Orozco & Campos-Filho, 2018	22	48	0	70
Total		598	218	51	867

Seasonal α-diversity and variables

The completeness of the sample, with a 95% confidence interval for the sampling sites, was 96.2% for the dry season, 100% for the transition season, and 99.5% for the rainy season. These values suggest that the sampling was representative across the three seasons (Fig. 2a). The abundance range curves exhibited low evenness between the seasons, with steeper curves during the transition and rainy seasons, indicating that seasonality affects the structure of the terrestrial isopod assemblage (Fig. 2b).

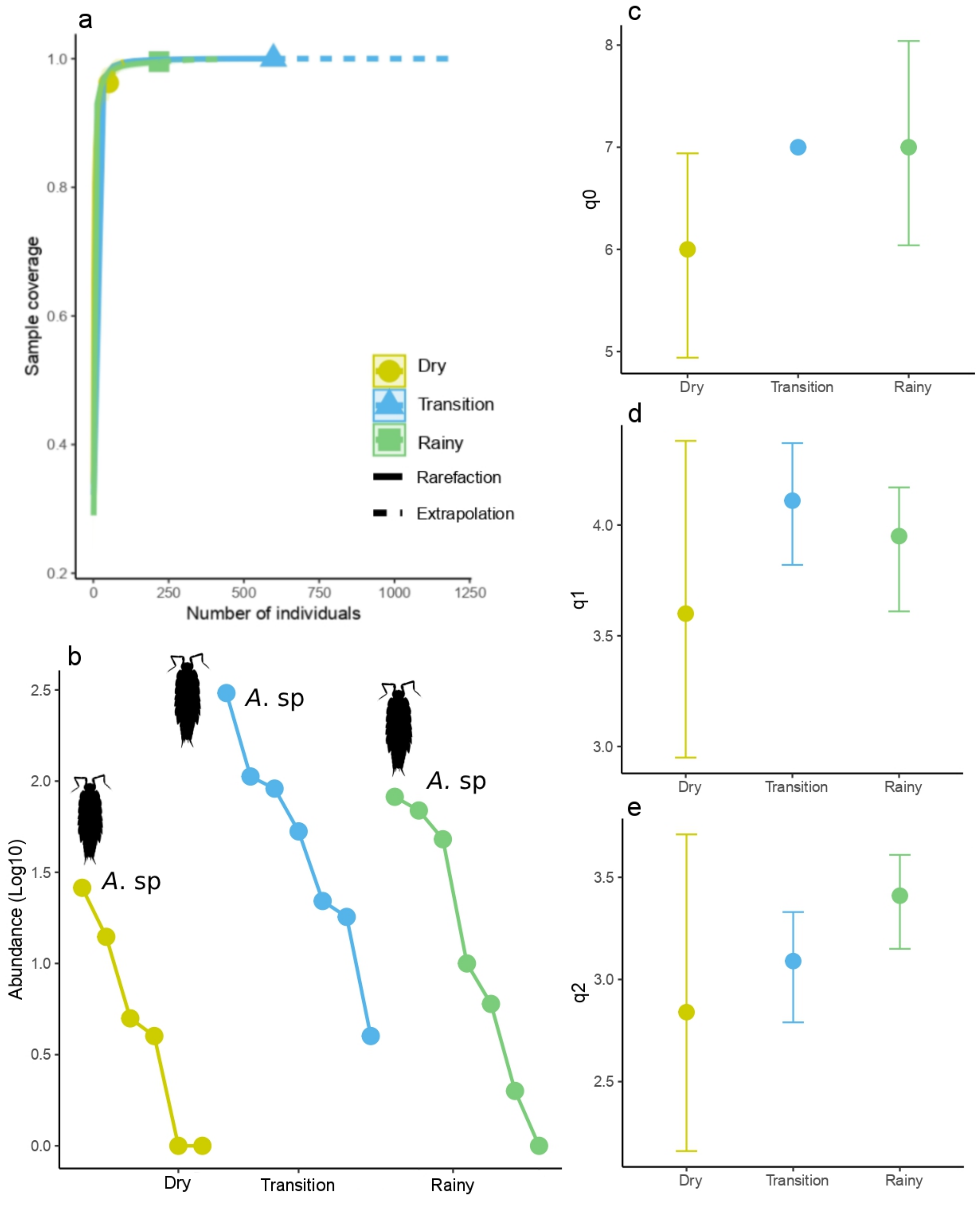

Fig. 2. (a) Sampling completeness of terrestrial isopods assemblage for climatic seasons. (b) Rank abundance curve of the assemblage of terrestrial isopods for climatic seasons, α-diversity profile for the three climatic seasons with 95% confidence intervals (*q* ± 95% CI), order *q*0 (c), order *q*1 (d), and order *q*2 (e).

Regarding alpha diversity, both the transition and rainy seasons exhibited the highest number of effective species (seven species each) (Fig. 2c). Meanwhile, the effective number of common species (*q*1) was observed during the transition season, followed by the rainy season (Fig. 2d). Dominant species (*q*2) were mainly represented during the rainy and transition seasons (Fig. 2e). Across all diversity orders, the dry season consistently showed the lowest values; however, the confidence intervals indicate that there are no significant differences between seasonality and diversity orders. Generalized linear models revealed that seasonality, soil temperature, litter temperature, and soil moisture significantly affect abundance. Litter temperature and soil moisture significantly influenced the diversity order (*q*0). Conversely, these variables did not present any significant effect on diversity orders (*q*1) and (*q*2) (Tables 2, S1).

Table 2. ANOVA test results of the generalized linear model on abundance of terrestrial isopods assemblage and diversity orders (Hill numbers) and variables. Likelihood ratio (lr x^2), degrees of freedom (*d.f.*)

Response variables	Explanatory variables	lr x^2	*d.f.*	*p*-value
Abundance	Seasonality	27	1	2.039e-07 ***
	Soil temperature	31.59	1	0.03212 *
	Litter temperature	110.78	1	2.2e-16 ***
	Soil moisture	324.09	1	2.2e-16 ***
*q*0	Seasonality	0.0356	1	0.8402
	Soil temperature	1.736	1	0.16363
	Litter temperature	5.5112	1	0.03794 *
	Soil moisture	8.8656	1	0.05041*
*q*1	Soil temperature	0.9355	1	0.158
*q*2	Soil temperature	1.01626	1	0.1122
	Litter temperature	1.7364	1	0.1813
	Soil moisture	2.3303	1	0.2245

Seasonal β-diversity and association with soil variables

The terrestrial isopod assemblage significantly differs between climatic seasons (Fig. 3a). Specifically, these differences were observed between rainy and dry seasons ($R^2 = 0.57$; $F_{\text{PERMANOVA}} = 8.17$; $p = 0.02$), and between transition and dry seasons ($R^2 = 0.57$; $F_{\text{PERMANOVA}} = 8.22$; $p = 0.02$). Total beta diversity between climatic seasons ($\beta_{\text{BC}} = 72.6$), was influenced by the balanced variation in abundance ($\beta_{\text{BC:BAL}} = 51.3$, 70.7%) (Fig. 3b), compared to the abundance gradient ($\beta_{\text{BC:GRA}} = 21.3$, 29.3%) (Fig. 3c). In other words, the structure of the terrestrial isopod assemblage varies across climatic seasons, primarily due to changes in the balanced variation of their abundances, indicating that there is a high rate of replacement of individuals (turnover) between climatic seasons.

Increasing soil environmental variables significantly increased total beta diversity between climatic seasons (Fig. 3d, e, f). Additionally, with increasing soil temperature and moisture, there was an observed a significative increase in the balanced variation component (Fig. 3g, h, i). The abundance gradient component of beta diversity was not correlated with soil variables (Fig. 3j, k, l).

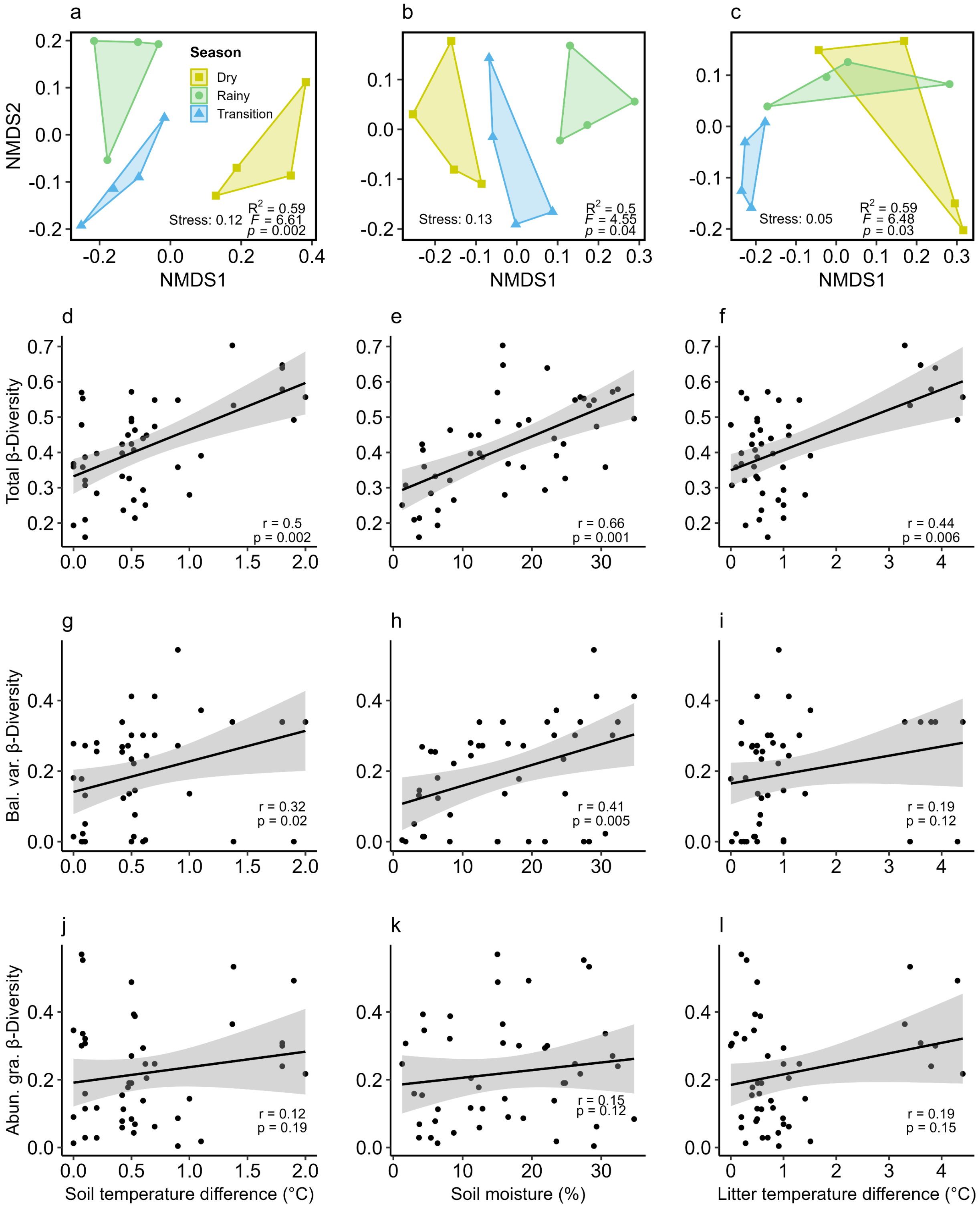

Fig. 3. Terrestrial isopods beta diversity and its components in Botanical Garden of Cartagena “Guillermo Piñeres”. Non-metric Multidimensional Scaling (NMDS) ordination analysis with terrestrial isopods assemblage between climatic seasons using total β-diversity (a), balanced variation of β-diversity (b), and abundance gradient β-diversity (c); relationships (Mantel test) between soil

temperature, soil moisture, and litter temperature with total β-diversity (d, e, f), balanced variation (g, h, i), and abundance gradient (j, k, l).

DISCUSSION

This study provides important insights into the diversity, composition, and seasonal dynamics of terrestrial isopod assemblages in the Colombian Caribbean Tropical Dry Forest (TDF).

Composition and abundance of the assemblage

Six terrestrial isopods species previously reported for the study area by Carpio-Díaz et al. (2018) were found. Additionally, based on the work of López-Orozco et al. (2016) and Campos-Filho et al. (2020), *Androdeloscia* sp. and *Ischioscia* sp. are a possible new species for science. Borja-Arrieta (2019) reported nine species in the Campo Aventura Roca Madre, a TDF area in good conservation status in the department of Sucre. The richness observed in Campo Aventura Roca Madre may be attributed to the well-preserved TDF cover, extensive vegetation, and diverse microhabitats it offers (Pizano et al. 2014). In contrast, the BGGP experiences greater environmental pressure due to urban development in its vicinity, which may explain why certain species found in Campo Aventura Roca Madre are either absent from the BGGP or occur in lower densities. Nonetheless, BGGP harbors an important proportion of the current terrestrial isopod richness associated with the TDF of the Colombian Caribbean.

The presence of *V. gigas* and *Ctenorillo dazai* Carpio-Díaz, López-Orozco & Campos-Filho, 2018 in all three seasons may be attributed to the physiological and ecomorphological adaptations of these species to arid environments. Generally, species within the Armadillidae family possess well-developed respiratory structures in their pleopods, enabling them to conduct respiration effectively in dry environments (Taiti et al. 1998; Paoli et al. 2002). Moreover, these species group exhibit eco-morphological characteristics that classified them as "Rollers" (Schmalfuss 1984); this conglobation capacity characterized by a convex body, helps reduce desiccation and predation pressure (Warburg 1987; Hornung 2011).

In contrast, species in the Philosciidae family are typically dominant in forested environments of the Neotropics and are commonly associated with microhabitats exhibiting high moisture levels (Araujo and Bond-Buckup 2005; Almerão et al. 2006). *Ischioscia* sp. was exclusively found during the rainy season, likely due to the high soil moisture characteristic of this period. Species within this genus are known to inhabit both secondary and primary rainforests at elevations of up to 2000 m, with their distribution influenced by soil moisture and litter depth (Leistikow 1999; Campos-Filho et al. 2020).

The results regarding the low abundance of *T. heterophtalma* align with findings by Quadros and Araujo (2008), who reported a low density of a *Trichorhina* (Budde-Lund, 1908) species in semideciduous secondary forests within Itapuá State Park, southern Brazil. In contrast, *T. bermudezae* was abundant during the transition season, consistent with the typical pattern of population peaks observed in terrestrial isopods at the onset of precipitation (Rushton and Hassall 1987; Kern and Köhler 2012).

Such variation in seasonal abundance reflects the diverse adaptations among isopod species in response to the distinct climatic conditions within the TDF.

Seasonal α-diversity of terrestrial isopods assemblage

Interestingly, during this study, no changes were identified in alpha diversity between seasons. This finding coincides with Almerão et al. (2006), who reported no variation in richness and equitability in the different climatic seasons in Brazil. These results suggest that, despite the marked seasonality of dry ecosystems in the Colombian Caribbean, which leads to species turnover between seasons, the ecological structure of the assemblage in the studied environments remains stable throughout the year. The replacement of species observed under the methods used may be attributed to adaptations of each species to environmental characteristic such as heavy rainfall or prolonged drought, potentially involving local migrations to adjacent areas or changes in microhabitat use (e.g., different soil layers, different vegetation strata) (Sfenthourakis and Hornung 2018).

The BGGP has a typical Gallery Forest, providing available organic matter year-round that serves as food for decomposer organisms. Additionally, it contains permanent bodies of water, potentially serving as a refuge for isopod species during the dry season and influencing the structure of assemblages. Almerão et al. (2006) also identify responses to anthropic pressure (such as trail visits and ecotourism), variations in vegetation cover, and floristic composition as determinants of isopod assemblage structure, all of which are relevant factors in the BGGP, an open space for visitors.

This study identifies changes in abundance throughout the three climatic seasons, which are associated with soil parameters and seasonality. Moreover, both litter temperature and soil moisture influenced the seasonal richness of terrestrial isopods. The high temperatures and low rainfall typical of the dry season in the TDF, likely restricted the activity of these organisms due to reduced food and shelter availability and adverse environmental conditions (Rushton and Hassall 1987; Leistikow 2001; Hassall et al. 2018), resulting in decreased numbers of individuals and species richness. Furthermore, the findings indicated that isopod populations maintained higher abundances during in the transition and rainy seasons, suggesting greater stability with increased humidity (Brigić et al. 2019). Several authors have noted that increasing soil temperature is associated with reduced absolute abundance of terrestrial isopod species, with population densities and reproductive aspects directly linked to soil physical variables (Araujo and Bond-Buckup 2004, 2005; Hornung et al. 2007; Quadros and Araujo 2007; Quadros et al. 2009; Kern and Köhler 2012; Lopes-Leitzke et al. 2013; Sokolowicz and Araujo 2013; López-Orozco et al. 2024).

Considering the above, the richness of terrestrial isopods in the TDF of the Colombian Caribbean remains consistent across climatic periods. However, increases in soil and litter temperature and decreasing moisture significantly impact assemblage abundance and richness. This behavior likely results from adaptive processes unique to each species, which possess specific ecomorphological and physiological characteristics enabling them to complete their life cycle in such environments. Generally, the distribution of terrestrial isopods closely correlates with soil moisture and habitat availability. Nonetheless, certain species may exhibit varied responses to environmental heterogeneity, reflecting the group's interspecific diversity (Sfenthourakis and Hornung 2018). An additional and under-documented aspect is the loss of individuals due to mortality from desiccation caused by environmental conditions, which could influence, albeit not significantly, the abundance dynamics of each species (Paris 1963; Sutton 1968).

β-diversity and association with soil variables

The assemblage of terrestrial isopods exhibited variations throughout the climatic seasons in the TDF, which were associated with changes in soil and litter temperature and soil moisture. These findings align with previous studies by Brereton (1957), Hornung and Warburg (1995), Khemaissia et al. (2012) and Lopes-Leitzke et al. (2013), which reported that seasonal climate patterns influence assemblage structure. Our results indicate that the beta diversity of the terrestrial isopod assemblage between climatic seasons was primarily affected by the balanced variation component of abundances (70.7%). This suggests that observed changes in assemblage structure between climatic seasons are mainly attributable to balanced variation in abundances, which correlates directly with changes in soil temperature and moisture.

According to Rushton and Hassall (1987) and Kern and Köhler (2012), soil temperature and moisture play key roles in determining these organisms' growth, survival, and reproduction. Optimal temperature and humidity conditions lead to population peaks. Generally, the transition and rainy seasons exhibited a higher abundance of terrestrial isopod species, with humidity percentages close to 39 and 41%, respectively. Overall, the soil arthropods assemblages of the TDF in the Colombian Caribbean demonstrate seasonal patterns closely linked to variations in precipitation, relative humidity and temperature (Ortega-Echeverría et al. 2019; García et al. 2021; Zapata et al. 2023).

Conservation implications in the context of environmental and climate changes

Terrestrial isopods are important components of soil fauna, playing an important role in the decomposition of organic matter, thereby contributing to soil formation and nutrient recycling (Zimmer and Topp 1999). They help accelerate the decomposition rate of organic matter (Ŝpaldoňová and Frouz 2014; Abd El-Wakeil 2015). Also, they serve as potential prey for various vertebrates, such as birds, mammals and amphibians, as well as for certain groups of invertebrates, including arachnids, insects, and myriapods (Araujo 1999; Paoletti and Hassall 1999). In agricultural contexts, they may even become emerging pests due to observed crop attacks (Waller 2012). Within the TDF, the BGGP represents a gallery forest habitat where terrestrial isopods, along with other edaphic arthropods, can access the necessary resources and environmental conditions (such as temperature and moisture) for their life cycle (Ortega-Echeverría et al. 2019; Zapata et al. 2023). Therefore, conserving this small but ecologically valuable portion of TDF in the Colombian Caribbean is crucial for preserving the biodiversity and ecological integrity of this ecosystem. Environmental changes and anticipated impacts of climate change, including more extreme weather events, rising temperatures, and altered precipitation patterns (IPCC 2014, 2018), pose significant threats to biodiversity in the Colombian Caribbean TDF, a unique and highly seasonal ecosystem (Gitay et al. 2002). These changes are expected to impact soil fauna, including terrestrial isopods, whose abundance and diversity contribute to ecosystem resilience, particularly in nutrient-poor soils that rely on decomposer organisms. The study's findings suggest that increased temperatures and reduced soil moisture due to climate change could decrease isopod richness and abundance, potentially disrupting essential ecosystem functions like nutrient cycling. In this context, BGGP represents an important conservation area within the Colombian Caribbean TDF, as it provides a stable refuge for isopods and other soil fauna. Safeguarding and managing this area is critical to maintaining biodiversity and ecosystem functions in the face of climate change. Protecting such habitats could help mitigate the impacts of climate fluctuations on soil communities, preserving their role in nutrient cycling and soil health.

CONCLUSIONS

The alpha diversity parameters of the terrestrial isopod assemblage from the Colombian Caribbean TDF did not exhibit temporal variations. However, the assessed soil physical variables and seasonality significantly influenced abundance. This pattern is supported by the physiological and ecomorphological adaptations observed in the species. The variables examined in this study strongly influence the seasonal dynamics of the TDF terrestrial isopod assemblage.

These findings have important implications for understanding organism dynamics within the TDF under environmental and climate change. Expanding sampling efforts to other habitats in the country where information on oniscideans is lacking, particularly in priority conservation areas, is essential. This expanded sampling will help assess these organisms' diversity, abundance, and seasonality, establishing a baseline for potential conservation, management, and sustainable use initiatives.

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Supplementary materials

Fig. S1. Study zone Native Forest of the Botanical Garden of Cartagena “Guillermo Piñeres”, Bolívar, Colombian Caribbean. (download)

Fig. S2. Study zone Arboretum of the Botanical Garden of Cartagena “Guillermo Piñeres”, Bolívar, Colombian Caribbean. (download)

Table S1. Generalized Linear Model (GLMs) summary to abundance and diversity orders (Hill numbers) of terrestrial isopods assemblage and variables. (download)