



Tree canopy enhances Collembola functional richness and diversity across typical habitats of the Gorongosa National Park (Mozambique)

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ABSTRACT

The role of tree canopies in protecting soil functional diversity is essential for ecosystems threatened by the longer lasting periods of drought, which are predicted to increase in the southern afro-tropical region. Nonetheless, biodiversity inventories of soil mesofauna are scarce in afro-tropical ecosystems, even in emblematic and well-studied protected areas, such as the Gorongosa National Park (GNP). Understanding the interrelationships between tree canopies and soil fauna functional diversity can provide insightful information for future adaptive management to protect wildlife and ecosystem services in the GNP, in the context of climate change. Here we assessed collembolan functional type richness and functional diversity in the dry period and during the rainfall across major GNP habitat types: miombo forests, mixed forests, and open savanna/floodplains. Besides the significant positive influence of rainfall, habitat types also influenced functional type richness and diversity of collembolan life-forms. Environmental gradients across habitat types, namely the area of tree canopy cover and its indirect effect on soil local conditions (pH and nutrient availability), explained collembolan functional parameters. Calcium concentrations and soil alkalinity significantly enhanced collembolan functional type richness and functional diversity, respectively. Collembola survival across GNP habitats depended on the canopy buffering in the dry sampling period. These results highlight the key role of tree canopies in creating suitable microhabitat conditions supporting soil functional diversity and the sustainability of soil processes and ecosystem services in GNP.

1. Introduction

Tree canopies support soil biodiversity and fertility underlying productivity in arid environments (Belsky, 1994). Their effects are especially relevant in typical grassland landscapes with scattered trees, such as Mediterranean agro-forests and Tropical savannas (Xu et al., 2011; Rossetti et al., 2015; Abdallah et al., 2016; Rutten et al., 2016). Tree effects on soil biodiversity may be a direct result of microclimatic abiotic conditions (e.g. air temperature, soil moisture conditions) due to canopy shading (Marañón et al., 2009; Xu et al., 2011; Widenfalk et al., 2015),

or indirect via the effect of leaf litter layers providing niche space and resource availability for soil fauna (Hättenschwiler and Gasser, 2005; Korboulewsky et al., 2016; Nascimento et al., 2019). This buffer role is critical in the context of climate change, as extreme climatic events are threatening soil communities in vulnerable ecosystems. A major environmental pressure are the longer lasting periods of drought which, along with human activities, are expected to increase habitat deforestation and soil desertification in the Mediterranean and Temperate regions (Lim et al., 2018), but particularly in tropical ecosystems (Khaine and Woo, 2015; Corlett, 2016; Mbokodo et al., 2020).

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In turn, soil fertility and functioning depend on key biodiversity components, namely soil fauna communities, in ecosystems under water stress (Lavelle et al., 2006). Among the different groups of soil fauna, the mesofauna - and notably Collembola - is important in terms of abundance and activity for regulation of decomposition and nutrient cycling (Hanlon and Anderson, 1979; Hopkin, 1997). The activity of Collembola species varies according to their eco-morphological traits linked to specific life-forms, e.g. euedaphics, hemiedaphics, epigeics (Hopkin, 1997; Potapov et al., 2020), and they are highly sensitive to changes in soil pH (Ponge, 2000; Rossetti et al., 2015; Martins da Silva et al., 2016; Rzeszowski et al., 2017) and moisture conditions (Verhoef and Van Selm, 1983; Pflug and Wolters, 2001; Makkonen et al., 2011; Harta et al., 2021). Conservation of the functional diversity of soil fauna is therefore an important issue for the protection of critical soil processes in tropical ecosystems. However, inventories of soil mesofauna, including Collembola, are still scarce in the afro-tropical region. Besides the extensive efforts made in South Africa (e.g. Barra, 1999; Barra and Weiner, 2009; Janion et al., 2011; Janion-Scheepers et al., 2015), soil biodiversity remains understudied in most African countries.

Therefore, we aimed to assess the effect of a tree canopy gradient on Collembola functional diversity of the main habitat types of Gorongosa National Park (GNP) in Mozambique. GNP has been an example in biodiversity conservation and restoration of emblematic mammal species (Stalmans et al., 2019), but soil fauna has been overlooked. GNP landscape comprises a diversity of habitat types, ranging from closed forests to more open savannas / floodplains (Massad and Castigo, 2016) and a marked seasonality (wet and dry seasons) with increasingly longer lasting drought periods (Kruger and Sekele, 2013). Hence, ecological research is needed on feedbacks between tree canopies and soil fauna functional diversity, for future adaptive management to the effects of climate change on soil fertility and desertification.

Previous studies showed that moister micro-climate conditions provided by tree canopies affects positively Collembola richness and influences community structure towards a higher relative abundance of euedaphic species (Martins da Silva et al., 2012, 2016; Salmon et al., 2014; Rossetti et al., 2015; Joimel et al., 2021). In contrast, the relative abundance of epigeics species is usually higher in open habitats, such as grasslands and open landscapes (Alvarez et al., 2000; Ponge et al., 2006; Martins da Silva et al., 2012; Salmon et al., 2014; Harta et al., 2021), as they are usually faster dispersers and more resistant to desiccation and disturbances in the upper soil layers (Verhoef and Van Selm, 1983; Alvarez et al., 1999; Ponge et al., 2006; Bokhorst et al., 2012; Salmon and Ponge, 2012). Yet, the findings above are focused on the Mediterranean, Temperate or Boreal regions. To our knowledge no studies were so far conducted to investigate the effect of tree canopies on soil fauna in tropical ecosystems.

Here we approached collembolan functional diversity based on community traits related to life-form, as a surrogate for Collembola taxonomic diversity (Reis et al., 2016; Winck et al., 2017; Joimel et al., 2021) and as a proxy for their functional role in soils (Malcicka et al., 2017; Potapov et al., 2020). Hence, effects of a tree canopy gradient on Collembola communities, in the dry period and after the rainfall, were addressed within three main hypotheses:

1. Besides the major influence of rainfall, different habitat types comprising different levels of canopy cover will be a driver of Collembola functional richness and diversity: we predict that a higher proportion of euedaphics will be found in more closed canopy environments in relation to open habitats;
2. Canopy positive effect on collembolan functional richness and diversity will be partly indirect via its influence on soil properties (e.g., pH, %organic matter, nutrient contents) due to increased local leaf litter;
3. Independently of the habitat type, the buffering effect of tree canopies will be more important to support collembola communities in the dry sampling period.

2. Material and methods

2.1. Study sites

Gorongosa National Park (GNP) occupies approximately 4000 km² of Sofala Province, in central Mozambique, at the southernmost end of Africa's Great Rift Valley (18°58'04.84" S, 34°21'41.64" E) (Stalmans et al., 2019). Annual minimum and maximum temperatures range on average between 15 °C and 30 °C, respectively (Herrero et al., 2020). The wet season in Mozambique lasts from November to April and mean annual rainfall within the Rift is 700–900 mm, peaking between December and February. Large areas of the Rift Valley are flooded after the peak rainfall, resulting in extensive floodplains around the central Lake Urema (Stalmans et al., 2019).

GNP encompasses a vast habitat diversity ranging from Afromontane rainforest (Mount Gorongosa, above 700 m elevation) and riverine forest, as well as wooded savannas and open floodplain at lower elevations (Massad and Castigo, 2016). Both higher and lower plateaus are covered with closed-canopy miombo forest dominated by trees of the genus *Brachystegia*. In the central part of the park ("lower Gorongosa") savannas range from "open" savanna (floodplain grassland) to "mixed" savanna (grass-shrub-open tree: transitional forest), as well as "closed" savanna dominated by several different tree species, i.e., mixed forests and miombo forests (Herrero et al., 2020). About 20 % of the valley's grasslands are flooded much of the year.

In this study we focused on the main three habitat types throughout the lower Gorongosa plateau, namely mixed forest, miombo forest and open-mixed savanna. These habitat types comprise an environmental gradient of inundation, from sites closer to lake Urema (open-mixed savanna sites), which are totally flooded in the wet season, to sites further from the lake and at higher elevation (namely miombo sites) (Table 1). Relative distances from each sampling site to lake Urema were calculated through Euclidean distances between spatial coordinates of each point and of the lake (mean distance per habitat type in Table 1). While this seasonal flooding is likely the main driver governing GNP ecosystem dynamics, a gradient of tree canopy density was also extracted across the three habitat types, with higher canopy density and leaf litter cover in mixed forest sites, and lower values in open-mixed savanna sites (Table 1).

2.2. Collembola sampling and processing

Field work was carried out in November of 2019 to capture the transition of the dry season to the first rains of the wet season, while avoiding the complete inundation of the habitat types selected for this study. We selected 75 sampling sites, at least 1 km apart, to avoid autocorrelation within and between the different habitat types: mixed forest, miombo forest and open-mixed savanna (25 sites each). Collembola sampling was carried out using PVC cylindrical soil cores with 5 cm diameter and 5 cm depth (98 cm³). Three sub-samples were collected with the soil cores disposed in a triangular shape (5 m apart) in the center of each sampling site.

First rains occurred on November 14th (40 mm) with heavy rainfall starting on November 20th (110–117 mm). Sampling dates were November 12th to November 14th (dry period) and November 22th, 24th and 27th (after the rainfall). Thus, part of the samples was collected during the dry sampling period and part after the rainfall (mixed forest: 17 in dry period, 8 after rainfall; open-mixed savanna: 14 in dry period, 10 after rainfall). Due to logistic constraints, samples from miombo habitat were collected only after the rainfall. During the soil core sampling, maximum temperatures in the GNP were in average 34.6 °C during October and 34.2 °C in November till the first rains. In the dry sampling period maximum temperatures were in average 35 °C, having decreased to an average of 30.3 °C during the wet season.

After sampling, soil cores were placed in Berlese-Tullgren extractors previously prepared in GNP facilities. Each soil core sub-sample was

Table 1

Site description of selected habitat types (mixed forest, miombo forest and open-mixed savanna) with geographical information (mean values \pm SD) and main environmental variables (mean values \pm SD) measured at the habitat and soil levels; “a” values of Euclidian distances between spatial coordinates of sampling sites and lake Urema; “b” values of the numerical classification (“0, 1, 3, 5”) corresponding to the categorical attributes “none, low, medium, high”; “c” diversity metrics based on habitat variables; “d” large mammal trace index. Variables in bold indicate those that were significant in the data analyses: “A” and “B” indicate groups separated by pair-wise Tukey HDS tests ($P < 0.01$) after ANOVA (canopy cover: $F = 9.80$, $P < 0.001$; litter cover: $F = 5.89$, $P = 0.004$; pH: $F = 30.2$, $P < 0.001$; %C: $F = 5.71$, $P = 0.005$; Ca: $F = 0.40$, $P = 0.673$).

		Mixed forest	Miombo	Savanna	
Geographic information	Latitude	-18.98 (0.02) 34.4	-18.99 (0.02)	-18.90 (0.01)	
	Longitude	(0.05)	34.2 (0.02)	34.4 (0.02)	
	Distance to lake	0.47			
	Urema ^a	(0.02) 34.4	0.48 (0.02)	0.39 (0.01)	
	Altitude (m)	(3.86)	97.3 (23.9)	25.6 (2.92)	
	Canopy cover (%)		58 (18.8)^A	31.1 (16.8)^B	29.8 (28.2)^B
			4.44 (0.90)^A	3.52 (1.42)^{AB}	2.88 (1.65)^B
	Litter cover ^b		2.92		
			(1.24)	3 (1.60)	3.42 (1.45)
	Herb cover ^b		1.52		
			(0.95)	0.72 (0.40)	0.42 (0.49)
	Shrub cover ^b		1.16		
			(0.90)	0.52 (0.50)	0.88 (0.80)
	Fallen trunks ^b		0.08		
		(0.15)	1.16 (1.36)	1.33 (1.31)	
Bare soil ^b		0.84			
		(0.40)	0.40 (0.48)	1.75 (1.04)	
Faeces ^b		1.20			
		(1.02)	1.48 (1.41)	2.83 (2.03)	
Trampling ^b		4.28			
		(0.58)	3.92 (0.67)	3.29 (1.09)	
Habitat Richness ^c		0.67			
		(0.06)	0.63 (0.04)	0.51 (0.15)	
Hab. Div. (Simpson index) ^c		0.83			
		(0.05)	0.83 (0.07)	0.83 (0.07)	
Habitat Evenness ^c		2.28			
		(1.55)	1.88 (1.40)	7.08 (4.18)	
Habitat variables	MT index ^d				
		6.01 (0.36)^A	5.94 (0.25)^A	5.25 (0.27)^B	
	pH (H2O)	49 (15.1)	65 (9.17)	32.4 (15.1)	
	Sand (%)	32.3			
		(12.2)	19.8 (8.07)	32.6 (7.44)	
	Silt (%)	18.6			
		(5.92)	15.2 (5.73)	35 (11.7)	
	Clay (%)	3.58			
		(0.53)	3.02 (0.55)	2.46 (0.86)	
	OM (%)	5.51 (1.94)^A	3.32 (1.15)^B	4.47 (2.04)^{AB}	
	C (%)	0.29			
		(0.14)	0.16 (0.04)	0.20 (0.05)	
	N (%)	60.1 (5.32)^A	62.2 (3.97)^A	50.7 (6.90)^B	
	Ca (cmol/dm ³)	18.3			
		(1.67)	18 (2.78)	20.1 (2.53)	
	Mg (cmol/dm ³)	0.03			
		(0.05)	0.01 (0.02)	0.30 (0.30)	
Al (cmol/dm ³)	85.6				
	(34.6)	41.8 (29.5)	23.9 (13.2)		
P (mg/dm ³)	4.72				
	(1.13)	3.29 (1.02)	2.76 (1.12)		
Soil variables	K (mg/dm ³)				

treated independently, and extraction time was four days per soil core: Collembola sub-samples were conserved in glass vials with pure ethanol and transported to laboratory in CFE - Centre for Functional Ecology in the University of Coimbra, Portugal.

2.3. Collembola sorting and life-form characterization

Collembola from all samples were sorted using a binocular microscope. All specimens were classified into different functional types according to a set of eco-morphological traits related to different Collembola life-forms in terms of adaptation to the soil profile: presence/absence of ocelli, length of the antennae, presence/absence (and length) of furca, presence/absence of scales or thick hairs along the body, and body pigmentation (Parisi et al., 2005; Vandewalle et al., 2010; Martins da Silva et al., 2016; Reis et al., 2016). Collembolan functional type classification was performed by attributing a score (ranging from 0 to 4) to each morphological trait (Supplementary Table S1). By comparing functional type scores with those obtained for a list of 270 collembolan species from a trait database (Berg et al. unpublished) we were able to assign each functional type as euedaphic, hemiedaphic or epigeic, based on Gisin classification (Gisin, 1960; Supplementary Table S1). Furthermore, after assigning the scores for each trait, a final composite life-form trait was calculated by summing up the partial scores of each functional type and dividing them by the maximum possible (20) so that each life-form trait varies between 0 and 1 (Martins da Silva et al., 2016). Hence, the higher the score, the higher the collembolan adaptation to the soil profile.

2.4. Measurement of environmental variables

2.4.1. At habitat level

At the center of each site, canopy density (variable: %Canopy) covering the sampling area was measured by image analysis of a photograph taken in the center of the triangle separating the three soil core' sub-samples. Imaging was performed using the Auto Threshold Plugin in ImageJ software, version 1.53e (Rasband 1997–2021). Also, a qualitative measurement of the presence and coverage of different habitat features (number of trees, leaf litter, shrub cover, herb cover, herb height, fallen trunks, bare soil, mammal trampling, mammal faeces) was performed within an area of 25m² enclosing the three sub-samples. Categorical data on the presence/amount of each habitat feature, categorized as “none”, “low”, “medium” or “high”, was numerically converted in “0”, “1”, “3” or “5” values, respectively, to use them as semi-quantitative variables.

Hence, “leaf litter”, “herb cover” and “shrub cover” were used in metrics of habitat diversity (Habitat richness, Shannon index, Simpson index and Evenness) based on the presence and relative amount of each of these three variables. Also, considering that soil fertility and levels of soil organic matter - important for Collembola communities - may be influenced by the density of large mammals (Rashid et al., 2017), an index based on large mammal traces (MT = trampling+faeces²) was calculated. Mean values of the habitat variables most relevant for data analysis are listed in Table 1.

2.4.2. At microhabitat level

Composite soil samples collected within each sampling site were used to determine several soil parameters reflecting microhabitat conditions, namely soil pH, organic matter content (OM), total N, C and organic C (%) contents; relative amount of important macronutrients (P, Ca, Mg, K, Al), cation exchange capacity (cmol dm⁻³) and base saturation (%); percentage of clay, silt and sand in soils; and soil type. All these measurements followed Tedesco et al. (1995)'s protocol. Average values of the most relevant soil microhabitat variables for data analysis are listed in Table 1.

2.5. Data analyses

Sub-samples from each site were pooled together. Then, for each site, the number of functional types (functional type richness - FS) was calculated. Also, the functional diversity ('FD' given by Rao's Q index) and the community weighted mean ('CWM') of the composite life-form trait based on functional type scores - of five single traits - were calculated using the *FD* package version 1.0–12.1 (Laliberté et al., 2014) implemented in the Statistical software R, version 4.1.2 (R Core Team 2009–2021). 'CWM' values corresponded to the mean value of a trait in the community, weighted by the relative abundance of the functional type carrying each trait score (Garnier et al., 2004).

A Repeated Measures ANOVA was used to test the effects of habitat type, controlling for the sampling period (dry vs. wet), on collembolan diversity parameters (FS, FD, CWM). Pairwise comparisons between habitat types were done by using Tukey HSD tests with Bonferroni corrections. FS and FD variables were log+1 transformed after checking the assumptions of homogeneity of variance among litter treatments (Levene's test) and of normality (Shapiro–Wilk tests). CWM variable did not need transformation to meet the assumptions of normality and homoscedasticity. Repeated Measures ANOVA were computed with the 'aov()' function in R. The confounding effect of spatially structured sampling sites was accounted for by running a previous selection model (GLM) using the 'vif' function from the *car* package version 3.1–0 (Lin et al., 2011) to check for collinearity and significance of lat-long coordinates. The fixed effects of spatial coordinates were not significant and thus they were discarded from further data analyses (Supplementary Table S2). Also, different groups of environmental variables, at the site (habitat) level and at the soil (microhabitat) level (Table 1), were inspected for collinearity and subjected to stepwise selection with the 'vif' function, after visual checking with a *pca* exploratory analysis performed with the *rcpp* R package version 1.0.8.3 (Eddelbuettel and Balamuta, 2018).

Effects of selected environmental variables at both levels were tested on response parameters (FS, FD, CWM) by performing General Linear Mixed Models (GLMM) fitted by the Restricted Maximum Likelihood (REML) estimation method. Habitat type and sampling periods were added to GLMM models as random factors, to extract the effects of environmental gradients independently of habitat and rain effects. Fixed effects were tested using the function 'anova' performed on the response variables and the fixed factors. All GLMM analyses were performed using the R packages *nlme* version 3.1–128 (Pinheiro et al., 2016) and *lmerTest* version 2.0–20 (Kuznetsova et al., 2014).

We addressed the causal relationships among the significant variables at the habitat and microhabitat levels on *Collembola* functional diversity parameters using structural equation modelling (SEM). As the focus was on the influence of canopy cover, we assessed its direct effect (shading effect) on collembola communities, but also the indirect cascade effects on local leaf litter amounts and the derived concentrations in key soil nutrients underlying soil pH (e.g., Noble et al., 1996; Reich et al., 2005; Tóth et al., 2011). In addition, we included the effects of rainfall, so our a priori global SEM predicted a direct effect of rainfall, canopy cover (shading), and soil properties (nutrient concentrations and pH), as well as the indirect effects of tree canopy, on collembolan FS and FD. Path diagram and SEM statistical information on path coefficients is provided in the Supplementary Table S3 and Supplementary Fig. S1. All SEM analyses were performed in R using the packages *OpenMx* version 2.20.6 (Neale et al., 2016), *lavaan* version 0.6–11 (Rosseel, 2012), *knitr* version 1.39 (Xie, 2014), *kableExtra* version 1.3.4 (Zhu et al., 2021), *semPlot* version 1.1.5 (Epskamp, 2019) and *GGally* version 2.1.2 (Schloerke et al., 2022).

Relationships between the canopy cover and *Collembola* response parameters were analyzed in separated seasons (dry period and after the rainfall). Zero-inflated models were used to test these relationships due to the excessive number of zeros generated by the split matrices, especially in the dry sampling period. Hence, a two-component mixture

model for count data (Hurdle model: Heilbron, 1994) tested both the presence-absence of functional types (binary model) among habitat types as well as examined the distribution of positive data (truncated Poisson) (Feng, 2021). Hurdle models were performed by using the *hurdlr* R package version 0.1 (Balderama and Trippe, 2017).

3. Results

A total of 980 collembolan specimens were collected across all study sites (41 % open-mixed savanna, 36 % miombo forest and 23 % mixed forest). The majority (89 %) of collembolan abundance was collected in after the rainfall with only a few (11 %) sampled in the dry period across habitat types. Total collembolan specimens were distributed in 27 functional types (23 in miombo, 16 in mixed forest, 15 in open-mixed savanna).

Collembolan functional type richness (FS) and functional diversity (FD) differed among habitat types (Table 2), with miombo sites recording significantly higher values than mixed forests and open-mixed savannas (Fig. 1a, b). Yet, *Collembola* FS and FD values were much higher after the rainfall relative to the dry sampling period (Fig. 1d, e). In general, samples were dominated by a few euedaphic and several hemiedaphic specimens, and no significant differences in CWM of collembolan life-forms were found among the three habitat types (Table 2, Fig. 1c), nor between sampling periods (Fig. 1f).

After the procedure of variable selection at habitat (site) and microhabitat (soil) levels, ten of each were selected to test the effects of environmental factors on collembolan FS and FD (Tables 3 and 4). GLMM using the sampling period and habitat types as random factors showed that tree canopy area was the only significant variable explaining differences in FS while the amount of litter explained differences in collembolan FD, at the habitat level (Table 3). At the microhabitat level, pH was the most significant variable influencing collembolan FS (Table 4), but the variables %Ca and %C also explained differences in FS among sites. FD was not significantly explained by any variable at the microhabitat level, but variables "Soil type" and "pH" were almost significant (Table 4).

Rainfall was the main factor directly explaining the increase in collembolan FS ($r = 0.70$) and FD ($r = 0.67$) in the structural equation models (Fig. 2a, b). The direct effect of pH also explained the increase of collembola FD (Fig. 2b), while higher collembolan FS were associated to higher calcium concentrations (Fig. 2a). In these path analyses the direct effect of canopy cover on FS and FD was not significant. Yet, along with soil type and calcium concentrations, tree canopy cover was significantly related to soil pH (Fig. 2a, b). Also, canopy cover explained the amount of litter which in turn (along with soil type) was directly related to calcium concentrations within sampling sites (Fig. 2a, b).

Hurdle models showed that the tree canopy factor supported significantly higher collembolan functional types after the rainfall, while

Table 2

Summary of the Repeated Measures ANOVA testing the fixed effects of GNP habitat types on *Collembola* functional type richness (FS), functional diversity (FD) and community trait weighted means (CWM) of collembolan life-forms, with the sampling period as error factor in the model (Df – degrees of freedom, SS – sum of squares, MS – mean squares).

Dependent variable	Habitat type	Df	SS	MS	F-value	P-value
FS	Effect	2	0.658	0.329	7.048	0.0016
	Residuals	70	3.267	0.047		
FD	Effect	2	0.010	0.005	5.575	0.0057
	Residuals	70	0.065	0.001		
CWM	Effect	2	0.117	0.058	1.524	0.2280
	Residuals	47	1.798	0.038		

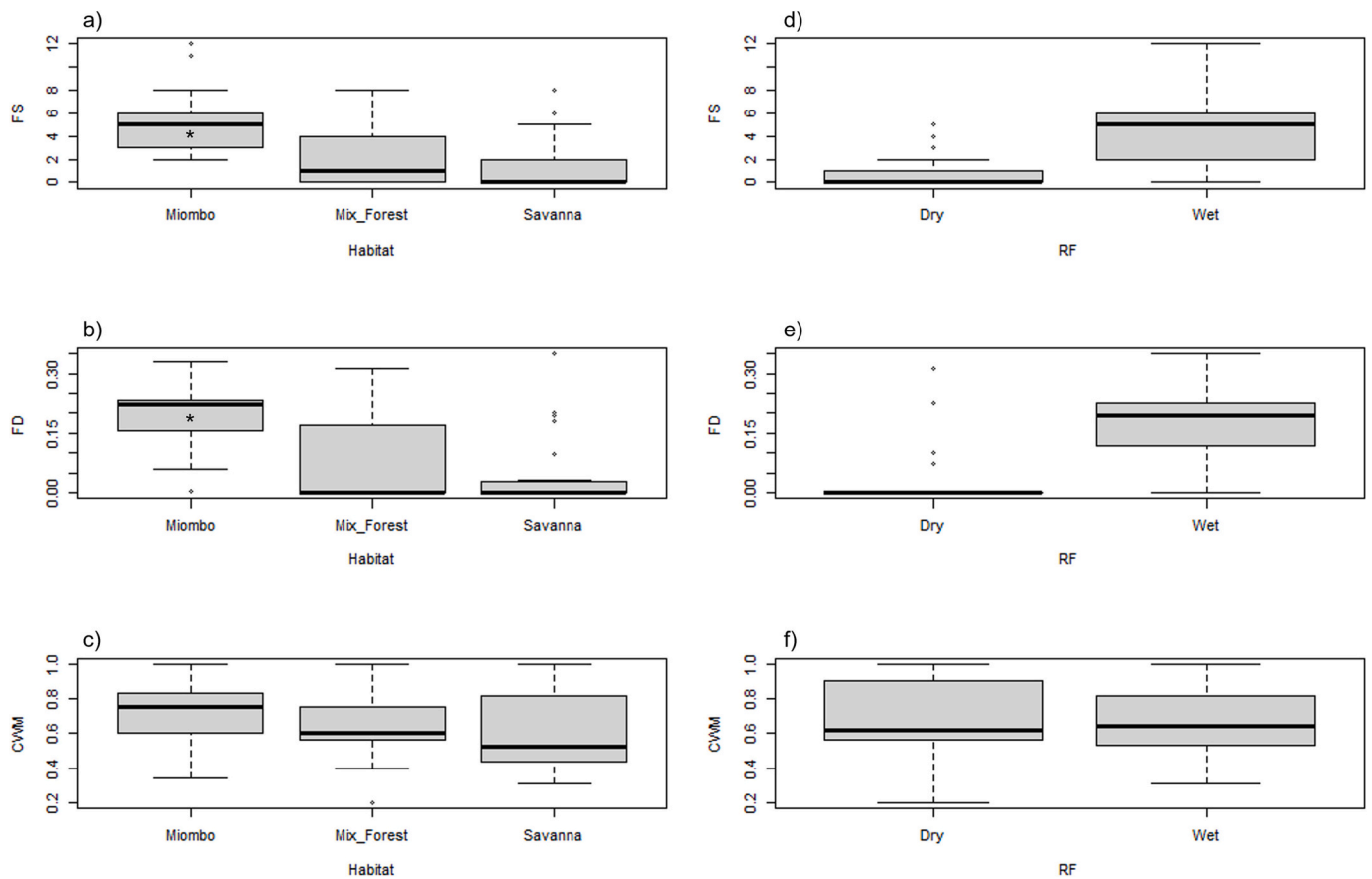


Fig. 1. Collembolan functional type richness (FS), functional diversity (FD) and community weighted mean of the composite trait of life-forms (CWM) of collembolan life-forms, recorded in the three studied habitat types (miombo forest - “Miombo”, mixed forest - “Mix_Forest”, and open-mixed savanna - “Savanna”) and in the two sampling periods (rainfall - RF: “Dry” and “Wet”). The asterisk indicates the habitat type significantly different from the others after pairwised Tukey tests ($P < 0.01$).

Table 3

Summary of GLMM analyses on the fixed effects of selected environmental variables at the habitat level for collembolan functional richness (FS) and functional diversity of collembolan life-forms (FD). Statistically significant results are in bold with F-values presenting the numerator (nDF) and denominator (dDF) degrees of freedom. Random effects variables: habitat types, sampling period.

	Fixed effects	nDF, dDF	F	p value
FS	Simpson index	1, 50	0.011	0.916
	Evenness	1, 50	0.628	0.432
	MT index	1, 50	1.827	0.183
	%Canopy area	1, 50	6.816	0.012
	N° trees	1, 50	0.001	0.970
	Bare soil	3, 50	1.378	0.260
	Herb cover	3, 50	0.657	0.582
	Shrub cover	2, 50	1.138	0.329
	Leaf litter	3, 50	0.480	0.698
	Fallen trunks	3, 50	1.732	0.172
	FD	Simpson index	1, 50	0.056
Evenness		1, 50	0.060	0.807
MT Index		1, 50	0.292	0.591
%Canopy area		1, 50	2.663	0.109
N° trees		1, 50	0.585	0.448
Bare soil		3, 50	0.373	0.773
Herb cover		3, 50	2.514	0.069
Shrub cover		2, 50	1.345	0.270
Leaf litter		3, 50	3.020	0.038
Fallen trunks		3, 50	0.519	0.671

Table 4

Summary of GLMM analyses on the effects of selected environmental variables at the soil level for collembolan functional richness (FS) and functional diversity of collembolan life-forms (FD). Statistically significant results are in bold with F-values presenting the numerator (nDF) and denominator (dDF) degrees of freedom. Random effects variables: habitat types, sampling season.

Response variable	Fixed effects	nDF, dDF	F	p value
FS	pH	1, 48	8.454	0.006
	P	1, 48	0.971	0.329
	K	1, 48	1.583	0.214
	Al	1, 48	0.388	0.536
	Ca	1, 48	4.412	0.041
	%C	1, 48	4.226	0.045
	%N	1, 48	0.107	0.745
	%Silt	1, 48	0.133	0.717
	Soil Type	3, 48	1.040	0.383
	Soil Class	9, 48	1.189	0.324
FD	pH	1, 48	3.149	0.082
	P	1, 48	0.321	0.574
	K	1, 48	1.022	0.317
	Al	1, 48	0.234	0.631
	Ca	1, 48	1.172	0.285
	%C	1, 48	0.166	0.686
	%N	1, 48	0.006	0.939
	%Silt	1, 48	0.000	0.997
	Soil Type	3, 48	2.592	0.064
	Soil Class	9, 48	0.955	0.488

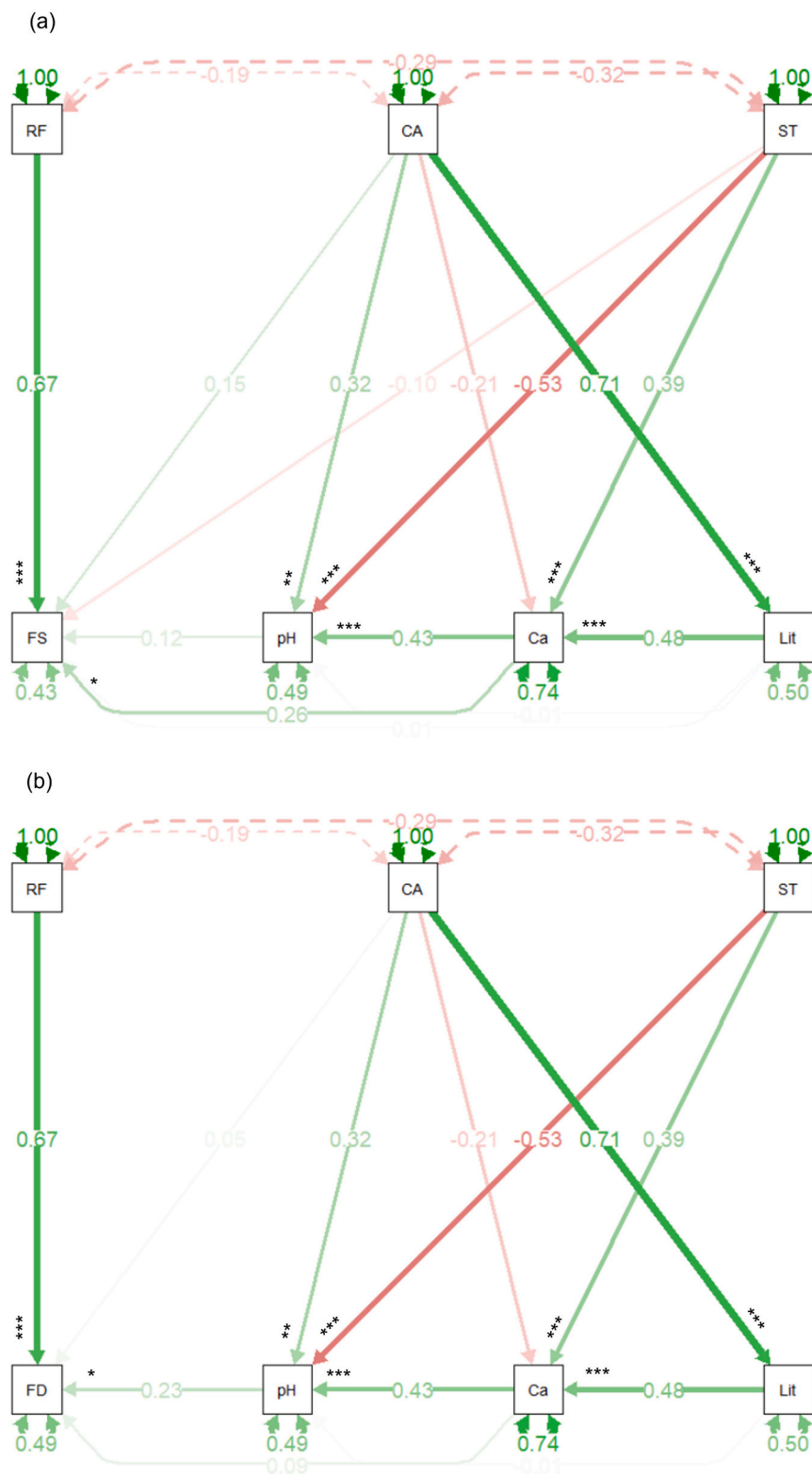


Fig. 2. Structural equation models (SEM) describing the influence of environmental conditions at the habitat (canopy area - “CA”) and microhabitat levels (pH values - “pH”, percentage of calcium - “Ca”), and the parallel effect of sampling period (rainfall - “RF”) on **(a)** functional type richness (“FS”) and **(b)** functional diversity of collembolan life-forms (“FD”). Arrows widths are proportional to the strengths of the path coefficients. Cascade effects of “CA” are investigated through the ensuing effects of the amount of leaf litter (“Lit”) on “Ca” and consequently on “pH”. Concurrent effects of soil type (“ST”) on “pH” and “Ca” are also explored in the SEM. Goodness-of-fit tests are: Collembola FS: $\chi^2 = 2.959$, $P = 0.706$; RMSEA = 0.0, $P = 0.780$; SRMR = 0.026; Collembola FD: $\chi^2 = 7.923$, $P = 0.161$, RMSEA = 0.089, $P = 0.245$, SRMR = 0.033 (** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

its effect on maintaining the presence of collembolan individuals was significant in the dry period (Table 5).

4. Discussion

4.1. Influence of habitat type and rainfall on Collembola functional parameters

In this study we showed that different habitat types may influence Collembola community structure in the Gorongosa National Park. We

Table 5

Summary of two-component mixture Hurdle models testing the singular effects of percentage of canopy area on presence-absence (binary model) and positive data (truncated Poisson) of collembolan functional type richness (FS). Statistically significant results are in bold.

Season	Response-Effect	Model	Estimate	SD error	Z value	p value
Dry	FS ~ %Canopy area	Count	-0.013	0.018	-0.717	0.473
		Binary	0.058	0.025	2.271	0.023
Wet	FS ~ %Canopy area	Count	0.009	0.005	2.007	0.045
		Binary	5.210	3502	0.001	0.999

recorded significantly higher values of functional type richness and functional diversity in the miombo forest in relation to the mixed forests and open-mixed savannas. Although this result is in line with our first hypothesis, it is difficult to disentangle the effects of habitat type and rainfall, given that miombo was only sampled after the rainfall. In fact, the effect of rainfall was clearly the main driver of collembolan communities, increasing functional type' richness of diversity across habitat types. This result was expected given the primary contribution of rainfall to soil moisture and fertility, especially in water-limited systems such as African savannas (Staver et al., 2017). Precipitation is a main driver of these ecosystems' dynamics (Herrero et al., 2020), influencing soil fauna communities, especially those strongly dependent on soil moisture and nutrient availability, like Collembola (Davidson, 1932; Hopkin, 1997; Lindberg et al., 2002; Krab et al., 2013; Rzeszowski et al., 2017). Still, we could depict the effect of environmental gradients related to habitat local conditions, namely the effect of tree canopy cover through its cascade effects on suitable soil properties and nutrients for Collembola communities.

4.2. Effects of main environmental gradients on Collembola life-forms

We expected that community traits of life-form would accurately indicate the influence of tree canopy on collembolan functional diversity. Based on previous observations in temperate and Mediterranean regions (e.g., Ponge et al., 2006; Salmon and Ponge, 2012; Salmon et al., 2014; Martins da Silva et al., 2016), we predicted that tree canopy influence collembolan richness and diversity in forested environments due to an increase in the relative abundance of euedaphics. Most euedaphics are expected to be particularly favored by local suitable microhabitat conditions promoted by closed canopy environments, as they are slower moving and are not equipped with traits protecting them against desiccation (Ponge et al., 2006; Bokhorst et al., 2012; Winck et al., 2017), such as larger body size or cuticular impermeability (Salmon and Ponge, 2012). Also, hemi- and euedaphics can migrate to deeper soil layers to avoid desiccation, while epigeic collembolans are generally more adapted to the drier soil surface holding thinner litter layers compared to forested sites (Alvarez et al., 2000; Makkonen et al., 2011; Martins da Silva et al., 2012; Salmon et al., 2014; Meyer et al., 2021). However, we found no significant increase in the proportion of euedaphics due to the canopy effect. Only a slightly higher, but not significant, proportion of epigeic species was detected in relation to the hemi- and euedaphics in the open savanna. Furthermore, no significant increase in the proportion of euedaphics collembolans was found in the soil cores after the rainfall event. It is possible that the combination of strong warming (not measured across habitats) combined with drought in the top layer caused a higher loss of surface-dwelling species relative to euedaphic species (Krab et al., 2013). Among epigeic collembolan life-forms, different species presented distinct tolerance levels to drought (Verhoef and van Selm, 1983) and temperature (Makkonen et al., 2011), and unlike the hemi- and euedaphic species they cannot escape the dry soil upper layers (Krab et al., 2013; Meyer et al., 2021). Previous studies

in Australia and Europe showed that epigeic Collembola may tolerate drought in a dormant egg stage for several months, hatching with the first rainfall of the wet season (Davidson, 1932; Wallace, 1968; Alvarez et al., 1999). Egg hatching, egg development and adult survival and activity depend largely on soil humidity levels (Wang et al., 2022). Likewise, it is plausible that in this tropical system most epigeic species remained also in a dormant stage during the long warm drought period. Previous experiments, in controlled laboratorial conditions, showed that collembolan dormant eggs hatch within 2 to 15 days after optimal temperature is reestablished (Leinaas and Bleken, 1983; Tamm, 1986), but hardly any study has focused on the time required for egg hatching with the reset of suitable moisture conditions (Holmstrup, 2019). Here we showed that a short period after the first rainfall, i.e., within eight days, was enough to restore the activity of a significant number of collembolan species that were in a dormant stage, either in egg diapause or anhydrobiosis (Sjursen et al., 2001).

Probably our results reflect the influence of other environmental gradients, namely the annual flooding, as the GNP savanna comprise a floodplain subjected to long periods of waterlogging caused by the annual inundation of the lake Urema (Stalmans et al., 2019). Such environmental stressor is expected to determine collembolan community dynamics and to select for species especially adapted to flooding conditions, such as euedaphic species in ecosystems subjected to periodic inundation (Widenfalk et al., 2015). Yet only few authors (e.g., Tamm, 1986; Marx et al., 2009) have addressed the flooding tolerance of Collembola species from different life-forms. These studies suggested that some epigeic species may also be adapted to waterlogging through egg diapause.

4.3. Tree canopy cascading effects on soil properties and nutrient contents linked to Collembola parameters

Independently of habitat type, tree canopy density increased functional type' richness and diversity of collembolan communities. We expected that tree canopy would be important not only due to the direct effect of shading, but particularly by altering soil properties linked to habitat suitability (e.g., soil alkalinity) and resource availability (e.g. nutrient concentrations) associated to the increase of leaf litter (Berg and Bengtsson, 2007; Martins da Silva et al., 2012; Salmon et al., 2014; Rossetti et al., 2015). Accordingly, our path analysis showed that the effect of canopy was not directly significant. Supporting our second hypothesis, the indirect effect of tree canopy – via enhancing local leaf litter – was significantly related to soil pH and calcium concentrations, which were directly explaining collembolan diversity across habitat types.

4.3.1. Soil pH

Previous studies from temperate and Mediterranean regions have found a negative correlation between collembolan diversity and pH across different habitat types, reflecting the higher richness of euedaphics in forest soils (Ponge et al., 2006; Rossetti et al., 2015; Martins da Silva et al., 2016). These are usually more acidic than grassland and agricultural ones (Hong et al., 2018), partly due to the production of organic acids from decomposing litter (Dijkstra and Smits, 2002). However, we found a positive relationship between pH and collembolan functional type richness, which results from the lower pH values recorded in the open savanna compared to the miombo and mixed forest soils. Through our path analysis we verified that the direct effect of pH was stronger on functional diversity of collembolan life-forms, probably reflecting the pH filter effect on particularly dominant euedaphic species that might be less tolerant to the acidic levels (Ponge, 2000). Also, some epigeic collembolans have showed a preference for subneutral pH conditions (Van Straalen and Verhoef, 1997).

The higher acidity of forest soils depends not only on the recalcitrant organic matter provided by thick leaf litter layers (Nilsson et al., 1982) but also, and primarily, on parent rock, soil type and inherent soil

chemical properties (Tamm and Hallbäck, 1988; Rossetti et al., 2015). Accordingly, we verified that soil type and texture influenced pH values, which were generally low (in average below 6) across GNP landscape. More importantly, we found that the density in canopy cover across habitat types was a determinant factor raising pH values, contrarily to the notion that open grasslands promote more neutral or alkaline soils than forested soils. In fact, the influence of afforestation on soil pH is still poorly known and in a recent study Hong et al. (2018) found that a significant soil pH neutralization was due to afforestation. The authors argued that afforestation may raise the pH in relatively acid soils, which is the case of the habitat types sampled in the GNP landscape.

The low general pH values, with especial incidence in the open savanna and transitional forest habitats, may be attributed to the effects of drought-post drought dynamics in floodplains. Fluctuations between soil inundation (due to heavy rain) and extreme drought are chief drivers of spatiotemporal changes in soil properties underlying biogeochemical processes (e.g. Schulz-Zunkel et al., 2015) with an influence on the pH of floodplain soils (Mosley et al., 2014; Ponting et al., 2021). Particularly, ecosystems with high abundance of organic matter and sulfate levels may suffer stronger drought-induced soil acidification along time (Mosley et al., 2014).

4.3.2. Calcium concentrations

Soil calcium is one of the secondary macronutrients required for plant growth, playing a role in the maintenance of soil physical properties, soil fertility (Dijkstra, 2003; Olego et al., 2021) and productivity in tropical forests (Baribault et al., 2012). Calcium

contributes to soil fertility through its mineralization and direct plant uptake (Dijkstra, 2003) but also by supporting life and the activity of decomposer and detritivore communities (Reich et al., 2005; Brown et al., 2013) which are important for nutrient cycling (Rzeszowski et al., 2017; Nascimento et al., 2019). Our results support this assumption, as we found that calcium concentrations were directly related to higher collembolan functional type richness values across habitat types. Higher concentrations of calcium in acidic soils may also influence functional diversity through its effects on soil pH (Duddigan et al., 2021). The importance of calcium for neutralization of soil acidity in forested ecosystems was demonstrated by previous studies (Noble et al., 1996; Dijkstra, 2003; Reich et al., 2005) and our results are in line with those findings.

Calcium uptake by plants and consumption by soil fauna depends largely on the amount of availability litter on soil surface (Dijkstra, 2003; Tóth et al., 2011). This was also confirmed by our path analysis, which found a significant positive effect of the amount of litter cover on calcium concentrations across habitat types.

4.4. Tree canopy importance in the context of climate change

Our results highlighted the importance of tree canopy cover in supporting Collembola life-forms in the GNP, either by increasing functional type richness and diversity in rainy periods and by significantly supporting the presence and activity of collembolans during the period of drought. Thus, in line with our third hypothesis, tree canopy appears to play a crucial role as environmental buffer against the drier surrounding environment. Local tree buffers support collembolan survival by preserving suitable microhabitat conditions and higher levels of organic matter and nutrient availability due to the higher amount of leaf litter (Lindberg et al., 2002; Martins da Silva et al., 2012, 2016; Rossetti et al., 2015).

In this case the provision of habitat refuge within Gorongosa landscape seems a key driver for soil fauna survival and diversity during the periods of drought, which are predicted to increase in Mozambique in the future (Massad and Castigo, 2016). Expected longer lasting periods of drought may contribute, in the long term, to the degradation of Gorongosa forested ecosystems and the shift towards more open woodlands (Massad and Castigo, 2016; Herrero et al., 2020). Hence, the

maintenance of tree canopy buffers is vital to sustain soil fauna diversity and, consequently the sustainability of key soil processes and services (Engelbrecht et al., 2007; Tóth et al., 2011) across the GNP landscape in the context of climate change.

Declaration of competing interest

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Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2023.105010>.

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