Diversity and Community Structure of Collembola (Hexapoda) across sites and microhabitats in the Bula Protected Area, a UNESCO-Listed Hyrcanian Forest at the Crossroads of Two Biodiversity Hotspots (Iran).

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Abstract

Background. The Hyrcanian Forests of Iran, a unique 850 km stretch of deciduous forest along the southern coast of the Caspian Sea, are renowned for their exceptional biodiversity, high levels of endemism and ecological integrity. The northern part of this forest massif is part of the Caucasian Biodiversity Hotspot, while its southern fringe extends into the Iranian-Anatolian Hotspot. The recognition of these forests as a UNESCO World Heritage Site has focused global attention on their protection, primarily from human disturbance. While the diversity of vascular plants is well documented, other groups, such as soil-dwelling arthropods, remain underexplored. This study aims to fill this knowledge gap by conducting inventories in different sections of the Hyrcanian forests, with a focus on Collembola, a potentially diverse but understudied group of soil fauna. The study was conducted to answer the following questions: Is the naturalness and degree of conservation of these forests reflected in the biodiversity of springtail communities? To what extent does the composition and diversity of these communities vary between different sites and micro-habitats within these forests?

Methods. To answer these questions, 89 samples were collected over a two-year period from three different forest sites that had undergone contrasting forest management. Specifically, the study focused on three forest ecosystems, a preserved anthropized (planted) forest (PAF), a preserved natural forest (PNF) and a non-preserved natural forest (NPF), all located in the Bula protected area. Three types of microhabitats were sampled at each site, including moss, litter and dead wood. The springtails collected were identified and counted (approximately 3,000 individuals in total), allowing various biodiversity indices to be calculated for the communities as a whole, as well as by site and microhabitat. Soil samples were also analysed to compare soil properties between the three sites.

Results. The results reveal an impressive diversity of springtails, with 73 morphospecies identified, belonging to 39 genera and 12 families. Of these, 49 could be identified to species level. The estimated total species richness ranged from 80 to 110 species. The analyses also revealed significant differences in species richness between sites, with two preserved sites (PAF and PNF) having a greater number of species compared to the non-preserved site (NPF), and in habitats, with greater diversity observed in dead wood, followed by soil and then mosses. A more detailed analysis of the communities showed a high degree of interspecific diversity in terms of abundance and distribution, without revealing strong patterns of ecological specialization for the majority of species. An analysis of cooccurrences showed that, in most cases species interactions appeared to be neutral. However, some pairs of species showed positive associations, while negative interactions were more marginal. The results of the soil properties showed no differences between the sites and no effect on the Collembola community.

Discussion. The Bula Forest host particularly diverse Collembola communities. The results underline the importance of conserving these environments, which harbours a high diversity of springtails. Additionally, the results highlight the crucial role of dead wood as a substrate in supporting this biodiversity. The results also call for a more in-depth investigation of the factors influencing the presence, absence and abundance of species, as well as an exploration of the underlying causes of positive or negative species covariation.

Keywords: Biodiversity, Dead wood, Ecological niche, Ecosystem, Forest management, Mesofauna, Microarthropod community, Spatial heterogeneity, Species co-occurrence, Soil fauna, Springtail.

Introduction

The Hyrcanian forests in Iran are a unique and ancient hardwood ecosystem stretching along the southern coast of the Caspian Sea, extending from Azerbaijan to Iran's eastern and northern provinces, including Guilan, Mazandaran, and Golestan (Akhani et al., 2010; Tohidifar et al., 2016). Dating back 25 to 50 million years, these forests served as major glacial refugia during the Quaternary glaciations, preserving numerous endemic species (Vakili et al., 2021).

Rich in biodiversity, these mountain woodlands provide essential ecological and economic services, such as groundwater conservation, wildlife habitat, and erosion control (Haghdoost et al., 2011). Key tree species

include *Fagus orientalis*, *Carpinus betulus*, and *Quercus castaneifolia* (Haghdoost et al., 2011; Mehrafrooz Mayvan et al., 2015a).

Despite their significance, the Hyrcanian forests have faced severe threats, losing about one third of their area since 1950, primarily due to human activities (Saeei, 1950; Tohidifar et al., 2016). Recognition as a UNESCO World Heritage site has raised global awareness of these forests, which are located in 15 regions, including Bula Forest (Tohidifar et al., 2016; Homami Totmaj et al., 2021) and are home to highly diverse natural communities (Naqinezhad et al., 2008; Vakili et al., 2021; Nourzad Moghaddam et al., 2018; Homami Totmaj et al., 2021).

Collembola (springtails), one of the earliest soil colonizers in the forests (Chahartaghi et al., 2005; Kuznetsova and Ivanova, 2020), play a crucial role in soil formation, nutrient cycling, and plant growth (Hopkin, 1997; Gange, 2000; Petersen, 2002; Filser, 2002). Local biodiversity of Collembola can be very high, reaching over 100 species per site and densities as high as 200,000 individuals per square metre have been recorded (Rusek, 1998; Hopkin, 2006; Harta et al., 2021). There are about 9000 published Collembola species worldwide (Bellinger et al., 2024) while Iran's share of this number was only 232 in 2020 (Shayanmehr et al., 2020) and reached 354 in 2025 (D'Haese et al., 2025). More than half of these species (250 species) were reported from Hyrcanian forests (D'Haese et al., 2025; Shayanmehr and Yahyapour, 2019). The number of published endemic species from these forests is on the rise (Shayanmehr et al., 2013; Yahyapour et al., 2020; Yahyapour et al., 2021; Yoosefi Lafooraki et al., 2020; Shayanmehr et al., 2013; Yahyapour et al., 2020; Yahyapour et al., 2021; Yoosefi Lafooraki et al., 2020; D'Haese et al., 2025; Shayanmehr et al., 2024). However, many species remain unknown in various areas of these forests, especially in the UNESCO-listed areas (Shayanmehr et al., 2020; Shayanmehr and Yahyapour, 2019; D'Haese et al., 2025).

The present study was conducted in the Bula Forest, a pilot site of the UNESCO-Listed Hyrcanian Forest, located in Mazandaran Province in the eastern region of Iran's Hyrcanian forests. We examined three sites within this forest, and three types of microhabitats within each site (Figure 1). A comprehensive inventory of the Collembola present in this forest massif was performed by sampling in the three sites above-mentioned with different forest management histories (a preserved natural, a preserved anthropized forest and a non-preserved natural forest) and within each site in three types of microhabitats, namely forest litter, dead wood and mosses. This sampling protocol was designed to explore the similarities and potential differences in springtail communities across various micro-ecosystems within the same geographic area.

This sampling enabled us to identify 73 morpho-species, belonging to 39 genera and 12 families. Of these, we were able to accurately identify 49 species. The list of these species and their precise description, illustrated with photographs, is the subject of a first publication, in which we have also summarized the specific diversity known to date of Hyrcanian forests (D'Haese et al., 2025).

Most studies on Collembola in Iran are qualitative faunistic surveys. Virtually no information is available on the diversity, density and on the structure of the communities of these soil animals. The only study worth mentioning is that done by Mehrafrooz Mayvan et al. (Mehrafrooz Mayvan et al., 2015a), in which the depth distribution of Collembola resembled that of temperate forests, whereby seasonal dynamics differed with highest densities in winter, indicating that reduced moisture in summer functions as a major determinant factor.

Specifically, we examine patterns of diversity and assemblage: (1) at a broad scale, across the entire study area; (2) at the intermediate scale of three distinct sites, each with a different forest management history and located within a few hundred metres of each other; and (3) at a finer scale, across three contrasting microhabitats within each site. This multiscale approach allows us to assess how local microhabitat variation—even within a single site—can support distinct Collembola communities.

More specifically, we want to address the following questions.

(1) Do these forests - internationally recognized for their ecological value and located at the intersection of two biodiversity hotspots – harbour particularly diverse Collembola communities?

(2) How does Collembola diversity vary among different forest sites and across distinct microhabitats (e.g. leaf litter, dead wood, moss)?

(3) Is the composition and evenness of Collembola communities consistent throughout the forest, or does it differ significantly between sites and microhabitats?

(4) Do Collembola species exhibit variation in abundance, spatial distribution, ecological preferences, or interspecific interactions—such as positive or negative associations with other Collembola species sharing the same habitat? Communities dominated by species linked by competitive interactions should exhibit numerous negative co-occurrence, resulting from species that segregate from each other. Conversely, positive co-occurrence could be a signed of shared microecological preferences or reveal mutualistic interactions such as syntrophy, which to our knowledge has never been studied in the field in Collembola.

(5) Do soil properties differ among sites, and if so, how do they influence Collembola communities within soil-associated microhabitats?

Material and methods

Sampling Protocol

The samplings were performed in the Bula Forest, which has a semi-humid climate and is located in the south of Do-Dangeh section of Sari (Mazandaran Province, Iran) and in the north of Khere-Nero (part of Alborz) mountain range (Figure 1). The Bula Forest has significant elevation differences in its various parts. The 3907 hectares of this protected area are covered with dense forests that are under the management of the Environmental Protection Organization of Iran (EPOI). The main vegetation types covering these territories are lowland deciduous forests, submontane and montane deciduous forests, Juniperus and Cupressus woodlands, cultural landscapes and artificial forests, riverine and valley forests (Akhani et al., 2010).

To broaden the chances of observing different species, and to provide a first assessment of the spatial variability of the Collembola communities, we took samples from three sites at various altitudes and undergoing contrasted forest management (Figure 1). The first site, at a higher elevation (1670 m a.s.l.), is pristine and undisturbed, representing a preserved natural forest (later called “PNF”). The second site, at a slightly lower elevation (1600 m a.s.l.), has been reforested as part of conservation efforts, classified as a preserved anthropized forest (“PAF”). Both of these sites are managed by the Environmental Protection Organization of Iran (EPOI), fenced off, and restricted from public access. The third site, situated at a lower elevation (1425 m a.s.l.), is open to the public and classified as a non-preserved forest (“NPF”).

Within each site, three types of microhabitats (dead wood, moss, soil and leaf litter) have been collected from various points, at about 30 steps apart. This was done twice, in late April 2021 and in early June 2022. As a total, within each site, three samples of soil and leaf litter, three samples of moss, and four samples of dead wood were collected in 2021 and between five and ten samples were collected in 2022. This amounts to a total of 90 samples (30 samples per site). It should be noted that we did not carry out any sampling in autumn, and it is possible that we missed a number of species that are particularly present at this time of year.

The soil and leaf litter samples were taken using a soil core (Ø 5 cm and at a constant depth of 0-10 cm). Moss and dead wood samples were collected in 500 mL plastic containers. The samples were tagged and transported in the afternoon to the laboratory and the soil fauna was then extracted using modified Tullgren extractors.

To study the soil physicochemical properties, three soil samples were collected per site, resulting in a total of nine samples. The soil analysis was conducted at the Soil Laboratory of Sari University of Agricultural Sciences and Natural Resources (SARU) to assess both physical and chemical properties. Physical properties included soil texture, determined by the percentage of clay, silt, and sand. Chemical properties included % organic carbon, % organic matter and pH.

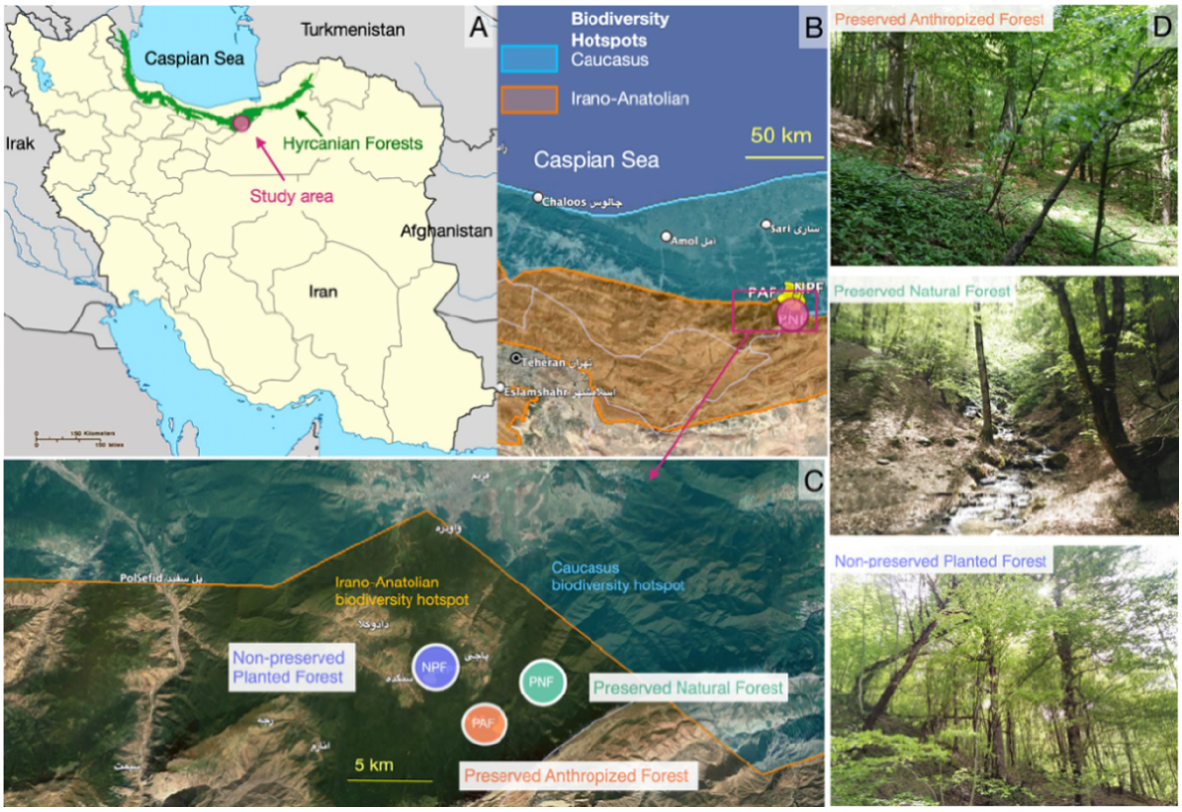

Figure 1 The general location of the study area located in the Bula Forest in northern Iran, Mazandaran is marked with a red circle on the Hyrcanian Forest (green) on a general map of Iran (A). A closer look (satellite maps B & C) shows the exact location of the three sites, a preserved anthropized forest (PAF), a preserved natural forest (PNF) and a non-preserved natural forest (NPF). These sites are formally located in the Irano-Anatolian Biodiversity Hotspot, but only a few kilometres from the border of the Caucasian Biodiversity Hotspot (Hoffman et al., 2016). The images on panel D show the general appearance of the three sites.

Collembola Sorting and Species Identification

For each sample, the specimens were examined under a dissecting microscope, sorted by morphospecies and, for each morphospecies, the number of individuals for each morphospecies was determined. The morphospecies were sorted according to shape and colour pattern. For species identification, some specimens were cleared in 10% KOH (for light specimens) and Nesbitt's solution (for dark specimens) and mounted in Hoyer's medium (Mari-Mutt, 1979). They were examined under a Nikon's ECLIPSE E600 microscope. Species were identified on the basis of morphological taxonomic characters described by Fjellberg (Fjellberg, 1998; Fjellberg, 2007), Potapov (Potapov, 2001), Jordana (Jordana, 2012) and Bellinger et al. (Bellinger et al., 2024). All materials are kept at the National Natural History Museum in Paris, France. The list and description of the species identified are published in two accompanying articles (D'Haese et al., 2025; Shayanmehr et al., 2024) and will not be discussed in detail here.

When the exact species name could not be determined, the morphospecies were named with their genus names followed by 'sp.'. The species names 'sp.01', 'sp.02'… were used to designate morphologically different morphospecies belonging to the same genus (D'Haese et al., 2025).

Some Neelipleones were present in the samples, but given their low numbers and rarity in some of the samples, compared to their expected density in such habitats, it has been assumed that most of them escaped the attention of the examiners during the sorting of the samples, especially from the first session (2021), and therefore we did not include them in some of the quantitative analyses (PCA). Similarly, some Symphipleones could not be accurately identified and are therefore not included in these quantitative

analyses either. On the other hand, a great deal of identification work was carried out on the Neanuridae, where almost all the specimens could be identified to species.

Statistical Analysis

Number of Specimens and Number of Species per Sample.

All the statistical analyses were performed using R (Ihaka and Gentleman, 1996) and we used the *ggplot2* package to constructs the figures (Wickham, 2009).

The mean number of Collembola per sample and the mean number of species per sample were analysed using quasi-Poisson generalized linear models (*glm* function), starting first with models that included the explanatory variables 'site' and 'habitat' and their interaction. These models were then simplified by removing the non-significant interactions (Faraway, 2016).

Species Diversity and Evenness

Before carrying out the species diversity analysis, we deleted the data where the springtails could not be assigned to an exact species or morphospecies. This includes certain damaged or juvenile specimens.

We carried out our analysis using a table with 479 rows, from which we were able to create a community data frame with 73 columns (different species) and 89 entries (we had 90 different samples, but in one of the samples no Collembola could be identified), using the function *matrify* from the R package *labdsv* (Roberts, 2023).

Species richness was examined using species accumulation curves plotted using the *vegan* (Oksanen et al., 2024) and *BiodiversityR* (Kindt and Coe, 2005) R packages. To compare species richness among sites and among microhabitats, we plotted species accumulation curves for the three sites and for the three habitats independently (Figure 4).

The expected species richness of the entire community (all samples pooled) was determined using the *diversityresult* function from the *BiodiversityR* package with different methods (bootstrap and first and second order jackknife gamma diversity estimator).

To compare the richness and evenness between sites and habitats, we used Rényi evenness profiles. These diversity profiles allow the comparison of species richness and evenness of communities at a glance. At scale 0, the estimated alpha reflects the species richness on a logarithmic scale. At scale 1 it corresponds to the Shannon index. At scale 2 it shows the Simpson index and for scale *inf* the Berger-Parker index is plotted. A flat profile indicates that the different species have the same evenness, while a declining profile is a sign of a community where species are unevenly distributed (Kindt and Coe, 2005).

Species Abundance and Ubiquity

To identify the species that were found to be the most abundant or the most ubiquitous among our samples, we sorted the morphospecies according to their total abundance (total number of individuals summed across all the samples, Figure 6A) and to their overall ubiquity which was determined as the proportion of samples in which each species was found (Figure 6B). These proportions and their 95% confidence intervals were determined using a Generalized Linear Model (GLM) model for binomial variables. We plotted the relationship between these two variables to graphically explore how the ubiquity and total abundance relate to each other, and to graphically show the dominant species in the studied forests.

Collembola communities, ecological specialization and species co-occurrence.

We used a principal component analysis to study the structuring of the Collembola communities using the *FactoMineR* and *factoextra* libraries (Lê et al., 2008; Kassambara, 2017). Specifically, we used this tool to look for any emerging structure in the samples according to the habitat type or sampling site.

We then used a graphical approach to look for any ecological preferences among the most common species, and finally we explored our dataset to study whether the presence of one species in a sample was associated with the presence or absence of another species. To do this, we used the *cooccur* package (Griffith et al., 2016), which is designed to classify the pairs of species as representing random, positive or negative associations. For example, a pair of species is classified as positively associated if the observed frequency of co-occurrence is significantly greater than the expected co-occurrence.

Results

Soil quality

Despite differences in forest management practices, the three sites had comparable soil composition (Figure 2A). Soil pH was also consistent across the sites, ranging from 5 to 5.5 (Figure 2B). The only notable difference was observed for organic carbon and organic matter. The soil of the preserved anthropized forest contained higher levels of organic carbon and organic matter compared to the other two sites (Figure 2B).

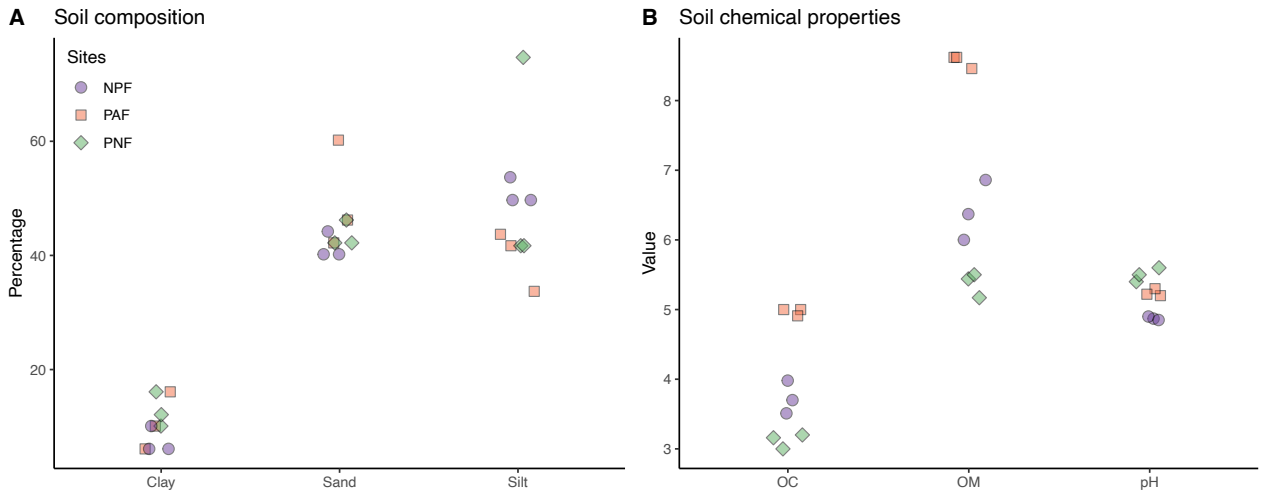

Figure 2 Soil composition was investigated by estimating the percentages of clay, sand and silt for three replicate samples within each of the three sites (panel A, NPF for Non-preserved Natural Forest, PAF for Preserved Anthropized Forest (PAF) and PNF for Preserved Natural Forest). We also report on panel B the measurements of three soil chemical properties (organic carbon OC, organic matter OM and pH) for the nine soil samples analysed.

Species Identified

From the 89 soil, moss and wood samples, we sorted 3095 specimens of Collembola which have been sorted into 75 different groups of "morphospecies". We removed two of these "morphospecies" from the diversity analysis because they grouped together individuals that were mainly juveniles or not recognizable enough to be attributed to something other than a genus (labelled "sp.") and we could not be sure that the individuals in these grouped belong to two or more than two species different from the other ones.

From the 73 remaining morphospecies, we managed to identify at the species level 49 of them (67%). The 24 remaining morphospecies have been identified at the genus level (labelled sp.01, sp.02…) and were visually sufficiently distinct to each other to form distinguishable morphospecies. Note that we found many *Tomocerus* juveniles in our samples and given that we only identified *Tomocerus minor* in the adults, we classified all these juveniles as *T. minor*.

The identified Collembola belong to four orders, 12 families - Entomobryomorpha (Entomobryidae, Isotomidae, Orchesellidae, Tomoceridae), Symphypleona (Katiannidae, Sminthuridae), Poduromorpha

(Hypogastruridae, Neanuridae, Odontellidae, Onychiuridae, Tullbergiidae), Neelipleona (Neelidae) - and 39 genera. The full list of species and their description is published in another article (D'Haese et al., 2025).

Collembola Abundance and Diversity in the Samples

We found an average of 34.5 specimens (median 24, range 1-150, Figure 3A) and 5.3 species per sample (median 5, range 1-14, Figure 3B). Using quasi-Poisson generalized linear models, we found that the site*habitat interactions were not significant for either Collembola abundance (χ^2_4=8.5, P=0.074) or species diversity (χ^2_4=1.5, P=0.82).

The simplified models without interaction showed that the total number of specimens and number of species per sample did not differ on average between the three sites (abundance: χ^2_2=1.37, P=0.50, diversity: χ^2_2=1.21, P=0.54), but differed between microhabitat types (abundance: χ^2_2=9.26, P=0.0097, diversity: χ^2_2=11.7, P=0.003): dead wood samples contained on average more springtails and more species than moss or soil samples, the latter two habitats not differing from each other (Figure 3 A & B).

Conversion of the number of specimens per sample into density, that is to say in number per square metre, was only possible for soil samples for which we know the sampling surface (Ø 5 cm). This resulted in a mean density of 12450 springtails.m^{-2} (95% confidence interval: 8900-16820 ind.m^{-2}).

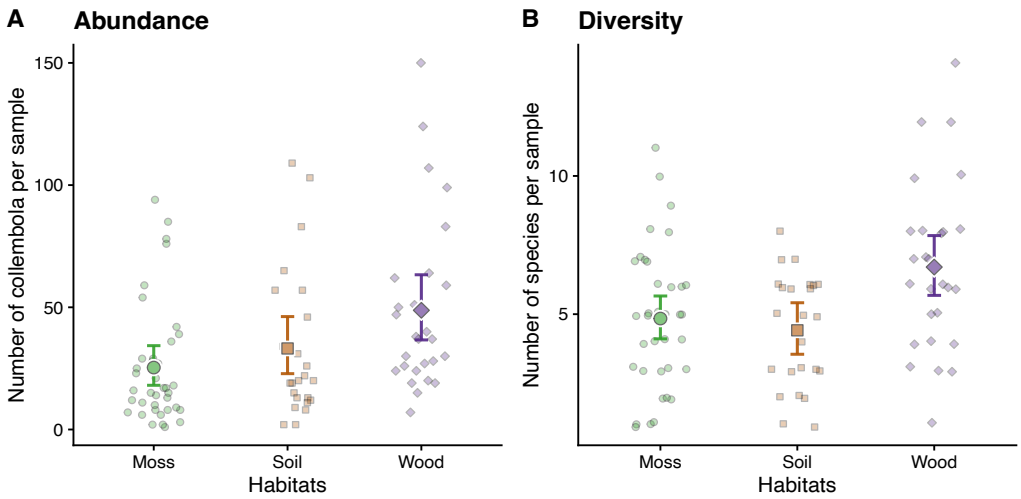

Figure 3 Number of Collembola (A) and number of species (B) per sample as a function of microhabitat type. The number of Collembola or species per sample is plotted for all samples (small dots), together with the mean and associated 95% confidence intervals derived from the simplified GLM quasi-Poisson models. On average, the number of individuals and species per sample is similar for soil and moss samples, but higher for wood samples.

Species Richness, Species Accumulation Curves and Measurements of Diversity.

The estimated extrapolated diversity is about 100 species for the three sites combined together (Table 1), although we have clearly under sampled certain groups of Collembola (D'Haese et al., 2025).

We identified more species in 2022 (53) than in 2021 (43), but this may be due to the greater sampling effort (30 samples in 2021 and 59 in 2022). In fact, the species accumulation curves of the two years largely overlap (Figure 4A), indicating that the overall diversity was the same between the two years. Given this observation, and the fact that our sampling protocol was not designed to allow a reliable comparison between years, we decided to group the two years together in the analysis.

Overall, we found slightly more species in the preserved anthropized forest (PAF, 51 species in total) than in the preserved natural forest (PNF, 45 species) and the non-preserved forest (NPF, 40 species, Table 1). The species accumulation curves diverged progressively among the three sites (Figure 4B), confirming the fact that the overall diversity varied slightly among the sites.

Regarding the microhabitats, the lower total number of species was found in the moss samples (33), while about the same number of species was found in the decaying wood (51) and in the forest soil and litter (47, Table 1). However, the species accumulation curves clearly show that, on average, dead wood is home to more springtail species than the other two habitats (Figure 4A), in line with what we observed in the samples (Figure 3B).

Table 1 Various measurements of species richness. The direct measurement of species richness is provided together with various estimates of extrapolated species richness, including the number of unobserved species. Chao's, first order jackknife and bootstrap estimators are accompanied with standard errors. The second-order jackknife estimators are given in brackets.

	Label	**Number of samples**	**Total number of species**	**Mean number of species per sample**	**Maximum number of species per sample**	**Chao's estimator**	**First order Jackknife estimator (second order)**	**Bootstrap estimator**
All samples together		89	73	5.3	14	109± 19	100±7 (116)	85±3.5
Sites	NPF	29	40	5.2	10	59±14	53±4 (62)	46±2.5
	PAF	30	51	5.7	14	74±13	73±6 (85)	61±3.4
	PNF	30	45	5	12	74±17	66±7 (79)	54±4
Habitats	Moss	24	33	4.4	8	55±15	47±5 (57)	39±2.5
	Soil	38	47	4.8	11	69±13	66±6 (77)	56±3.2
	Wood	27	51	6.7	14	77±15	72±7 (85)	60±3.8

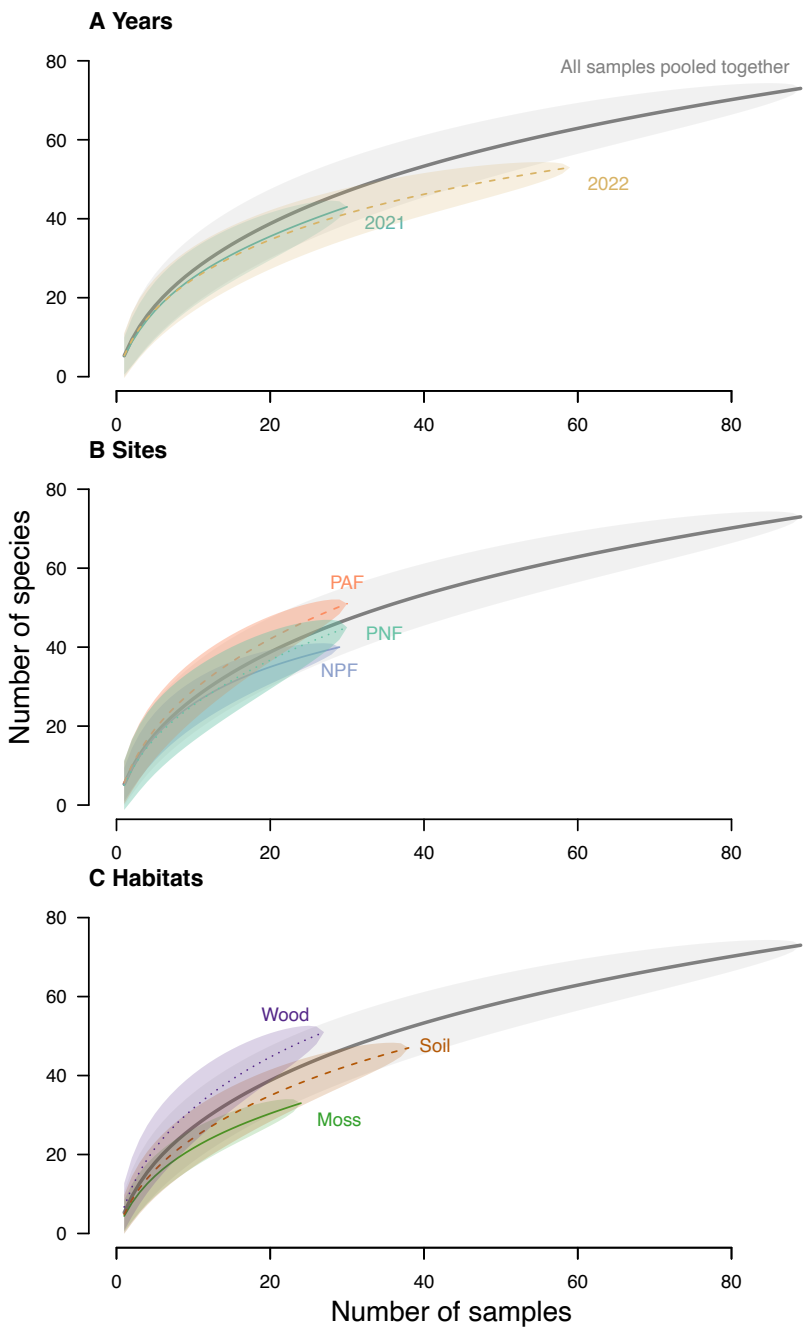

Figure 4 Species accumulation curves estimated using all different samples (grey lines) or different subsets of samples. Panel A shows the two years separately. Panel B allows comparison of the accumulation curves estimated for the three sites independently, namely Preserved Anthropized Forest (PAF), Preserved Natural Forest (PNF) and Non-preserved Natural Forest (NPF). Panel C shows the accumulation curves for the three habitat types (dead wood, soil or moss).

Richness and Evenness

When analysing species evenness using Rényi profiles, we found that the preserved natural forest site exhibited higher diversity than the other two sites (Figure 5A). In terms of microhabitat types, diversity remained consistently higher in dead wood compared to soil or moss across the entire gradient of species evenness incorporation into the diversity measure (Figure 5B).

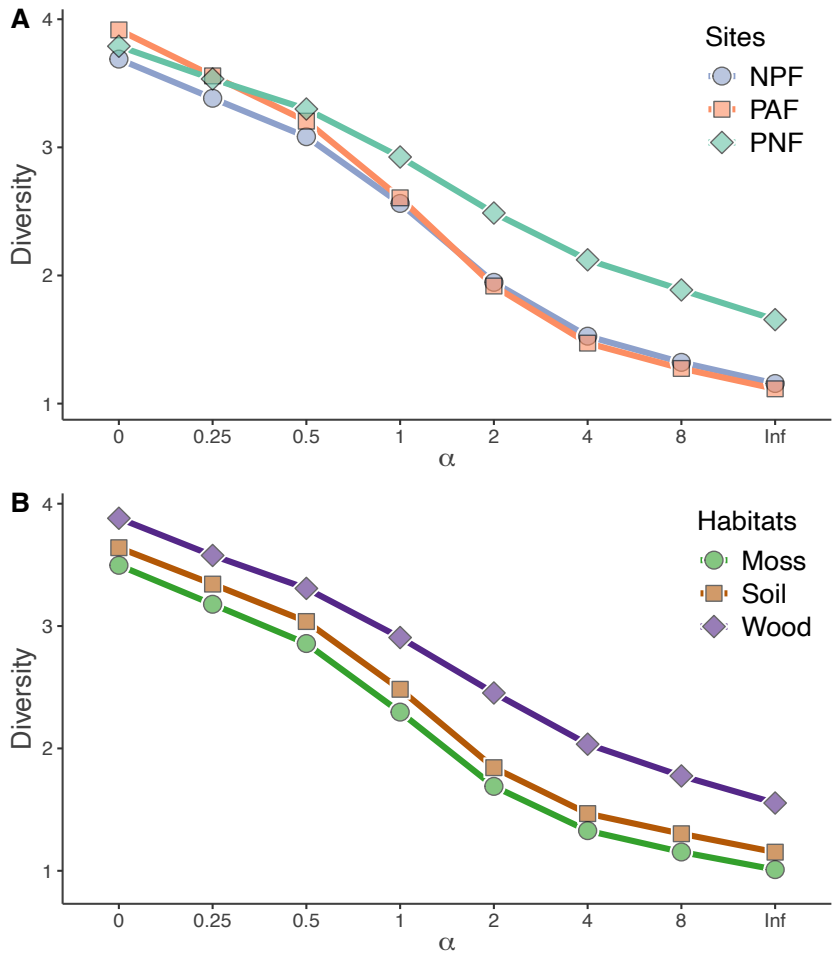

Figure 5 Rényi diversity profiles. Comparison of the three sites (A) and of the three habitats (B). The scale parameter (alpha) changes the influence of species richness and evenness on the measurement of diversity. For a scale of zero, the diversity is equal to the ln of species richness. For a scale of 1, diversity corresponds to the Shannon index.

Abundance and Ubiquity

When comparing species across sites, we found that *Seira domestica* was the most abundant, followed by *Folsomia peniculata*, a *Drepanura (sp.01), Heteromurus major, Ceratophysella stercoraria, Tomocerus minor, Orchesella cincta* and *Parisotoma notabilis* (Figure 6A). These species were both abundant and relatively ubiquitous, occurring in more than 20% of the samples. For instance, *Drepanura sp.01* was present in about half of the samples (Figure 6B).

These species were dominant in terms of both total abundance and ubiquity, appearing in more than 30% of the samples, with the exception of *Heteromurus major*, which was less ubiquitous than the other species (Figure 6B).

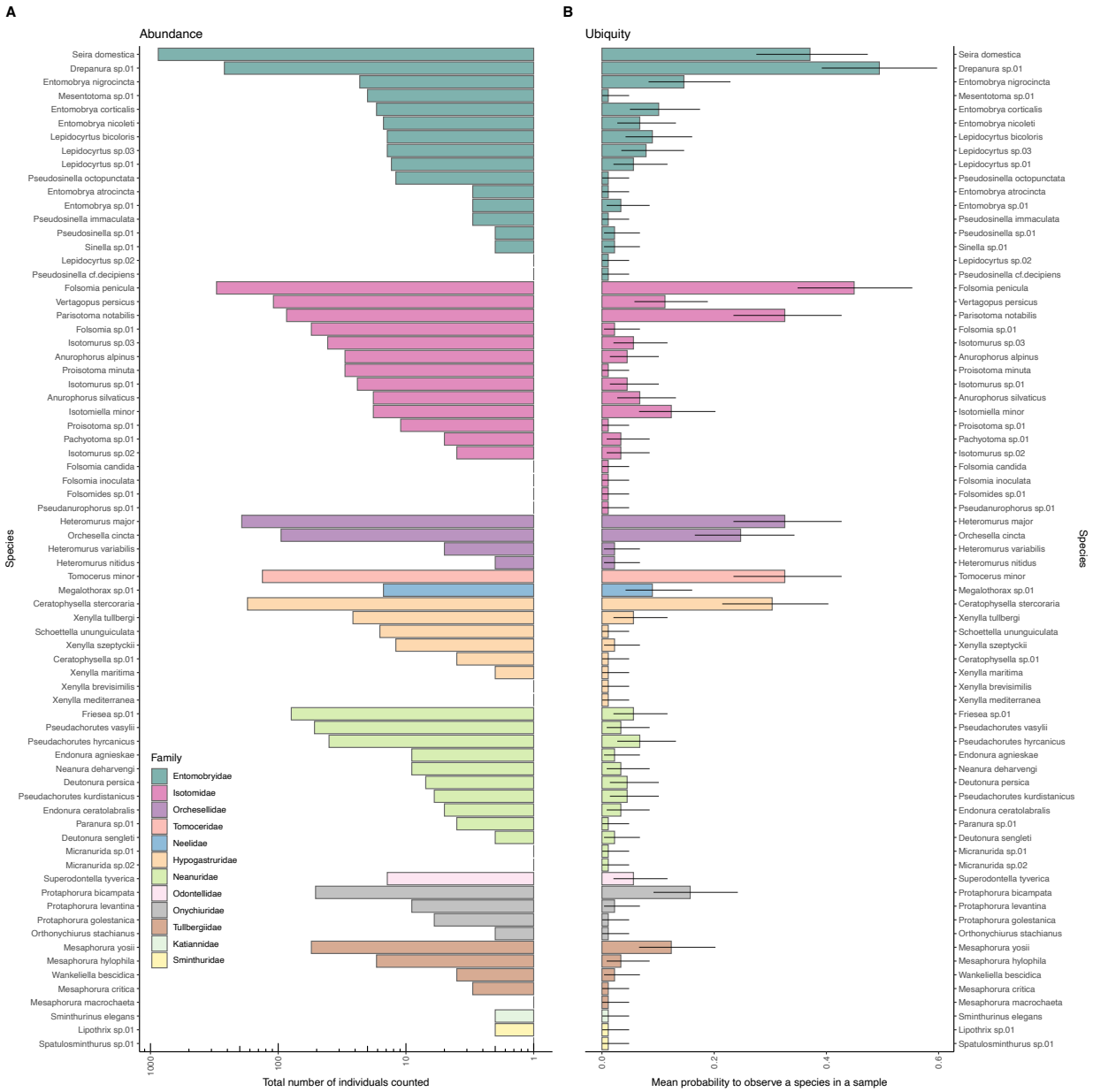

Figure 6 Panel A shows the total number of specimens collected for each morphospecies identified. Note that the number is plotted on a logarithmic scale. It corresponds to a rank-abundance curve, but the species have been grouped by families, which are highlighted in different colours. Panel B shows, for each species, the proportion of samples in which we observed the species. The grey bars represent the 95% confidence intervals for each estimated proportion. The species are ordered from top to bottom by order, family and decreasing total abundance.

The relationship between the ubiquity of each species and their abundance was examined in more detail using Figure 7. Ubiquity was defined as the proportion of samples in which the species was observed. Abundance was assessed at two different scales : (1) at a global scale (Figure 7A), abundance was defined as the total number of individuals for each species across all samples, as shown in Figure 6A. (2) At a local scale, abundance was calculated as the average number of individuals in samples where the species was present, focusing only on those specific samples (Figure 7B).

We found that, although on average ubiquity increased with global abundance (Figure 7A), this relationship was far from (log)linear. In fact, we found a group of relatively rare species, present in less than about 10% of the samples, for which we found no relationship between abundance and ubiquity (flat relationship).

Some were both rare and locally scarce, while others were rare but locally relatively abundant (e.g. *Friesea sp.01*, *Folsomia sp.01*, Figure 7). In another group of species, the ubiquity increased with overall abundance: from *Protaphorura bicampata* and *Mesaphorura yosii* to the ubiquitous and dominant *Seira domestica*, *Folsomia penicula* and *Drepanura sp.01* mentioned above (Figure 7A). When considering abundance at a local scale (Figure 7B), a species – *Seira domestica* - stands out for being both globally ubiquitous and locally abundant, a "common species" in other words. The other species form three main groups. The largest group includes species that are both rare and small in number when present: rare species. There are also species that are locally scarce, but present in a large proportion of the samples. Examples of these sparse species include *Folsomia penicula*, *Tomocerus minor*, *Heteromurus major, Parisotoma notabilis*... Finally, some species, such as *Proisotoma minuta*, *Pseudachorutes vasylii*, or *Schoettella ununguiculata* are infrequent but relatively abundant when present.

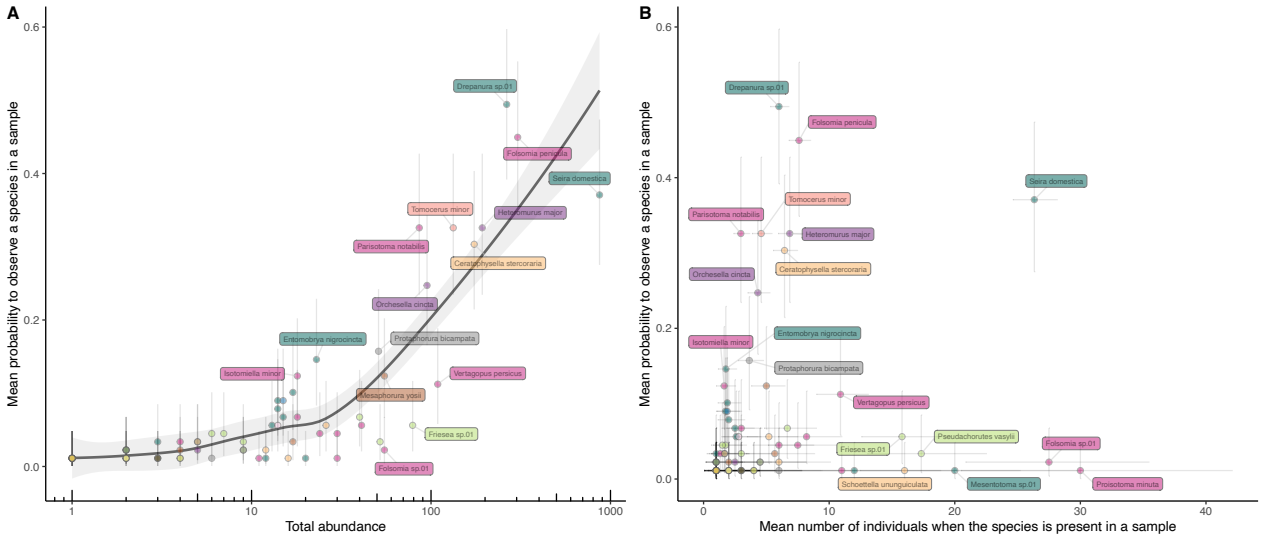

Figure 7 This figure shows the relationship between species ubiquities, expressed as the proportion of samples in which the species was observed, and species abundances. The abundance has been measured either by summing per species all the Collembola collected in the different samples (Total abundance, A), or by averaging the number of individuals in the samples in which the species is present (local abundance, B). The colours represent the different families (see Figure 6) and the error bars represent the 95% confidence intervals estimated by the GLM models used to measure the ubiquity (binomial model) or local abundance (Poisson model).

Collembola Communities

We then used a principal component analysis to search for some potential structuration of the Collembola communities between sites and habitats (Figure 8 & Figure 9). In this analysis, we excluded the species that were present in very few samples and retained those that were present in at least 10% of the samples (13 species).

The first two axes captured 31.8% of the total variation. On this projection plan, three groups of Collembola emerged (Figure 8). The first group associates *Entomobrya nigrocincta* with *Seira domestica,* which may be related to the fact that *E. nigrocincta*, despite having much lower densities than *Seira domestica*, is almost always found in association with *S. domestica*. The second group includes *Tomocerus minor*, *Orchesella cincta*, *Heteromurus major* and the relatively locally abundant but less common *Entomobrya corticalis*. Finally, in the third group we find two Isotomidae (*Isotomiella minor* and *Folsomia penicula*), *Protaphorura bicampata* and *Mesaphorura yosii*. *Parisotoma notabilis* lies between the second and third group. Note that some rather common species such as *Drepanura sp.01*, *Ceratophysella stercoraria* contributed only marginally to these two main axes, which is consistent with the fact that the two main axes captured only slightly less than a third of the total variance.

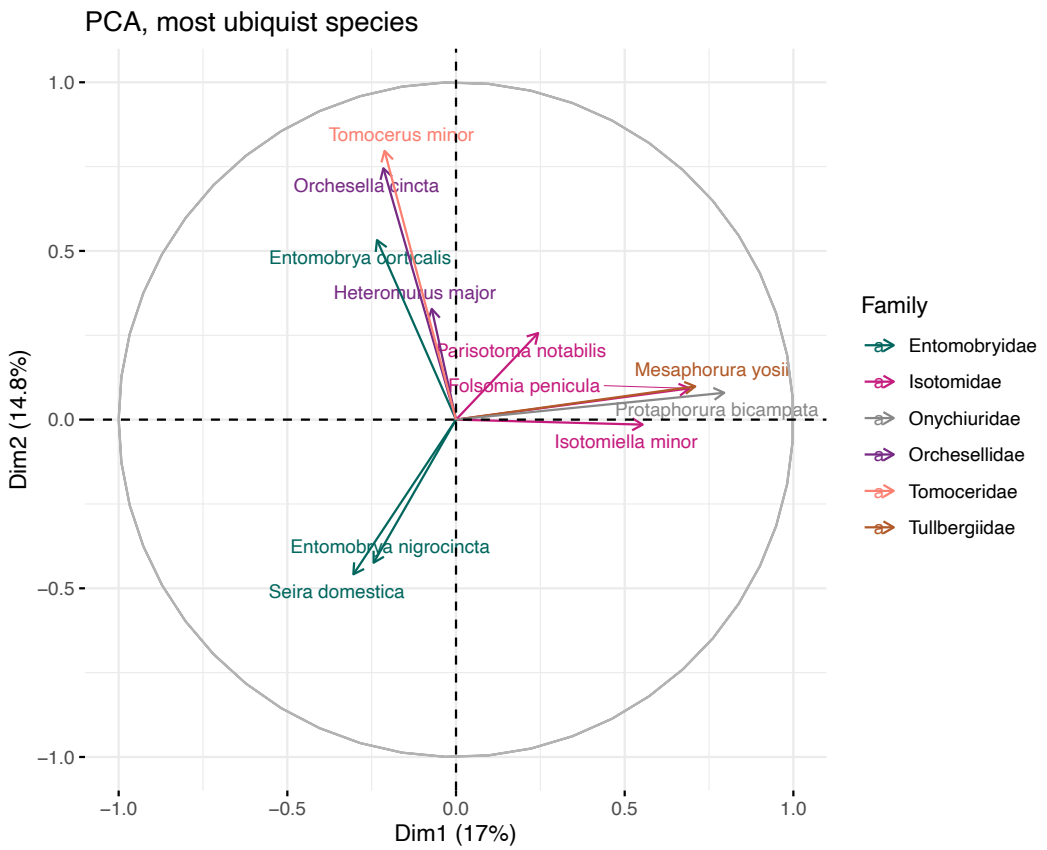

Figure 8 Principal component analysis of the most common species. The different colours indicate the different families.

When we plotted the samples on these two axes (Figure 9), we found very little community structuring between microhabitats (Figure 9 A, B) or between sites (Figure 9 C, D). In terms of microhabitats, a closer look at the scatterplot suggests a slight structuring of the moss samples compared to the wood and soil samples. However, there was definitely no structuring between the three sites (Figure 9 C, D).

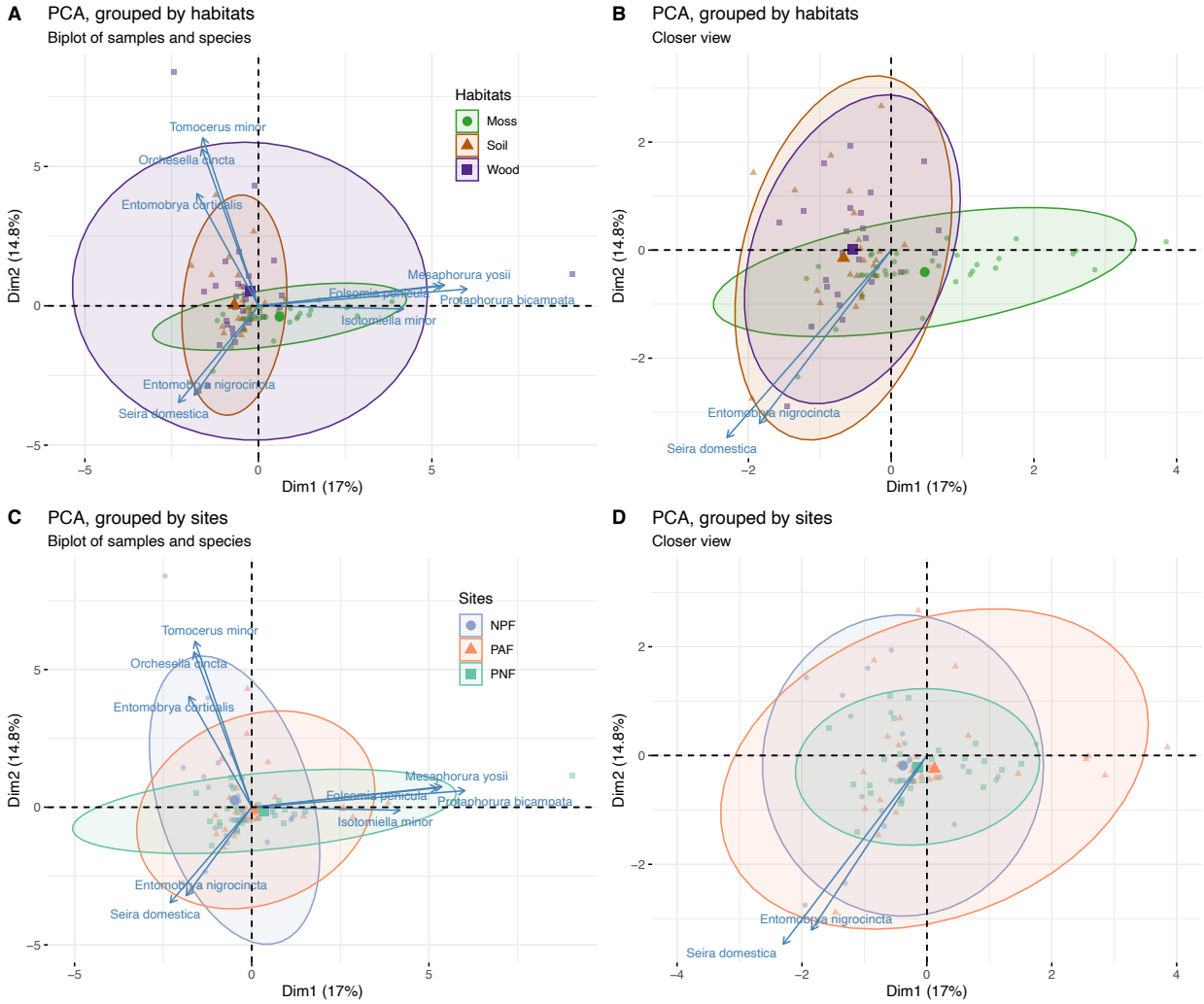

Figure 9 Principal component analysis. The ten species that contribute most to the first two axes are plotted, the contribution of the remaining species being negligible. The samples are plotted and grouped by either microhabitat type (A, B) or sampling location (C, D) using colours and ellipses. The figures on the right (B, D) show a closer look at the centre of the scatterplots of the corresponding figures on the left.

A representation of the occurrence of each of the species within the three microhabitats allows us to better understand the weak structuring of the communities by microhabitat revealed by the principal component analysis. Figure 10 shows that the ten most common species are present in all three microhabitats. It is only for the less common species that we can detect a more or less strong specialization towards certain microhabitats: *Isotomiella minor* was, for example, almost exclusively present in mossy habitats, while *Lepidocytus sp.03* was mainly observed in dead wood.

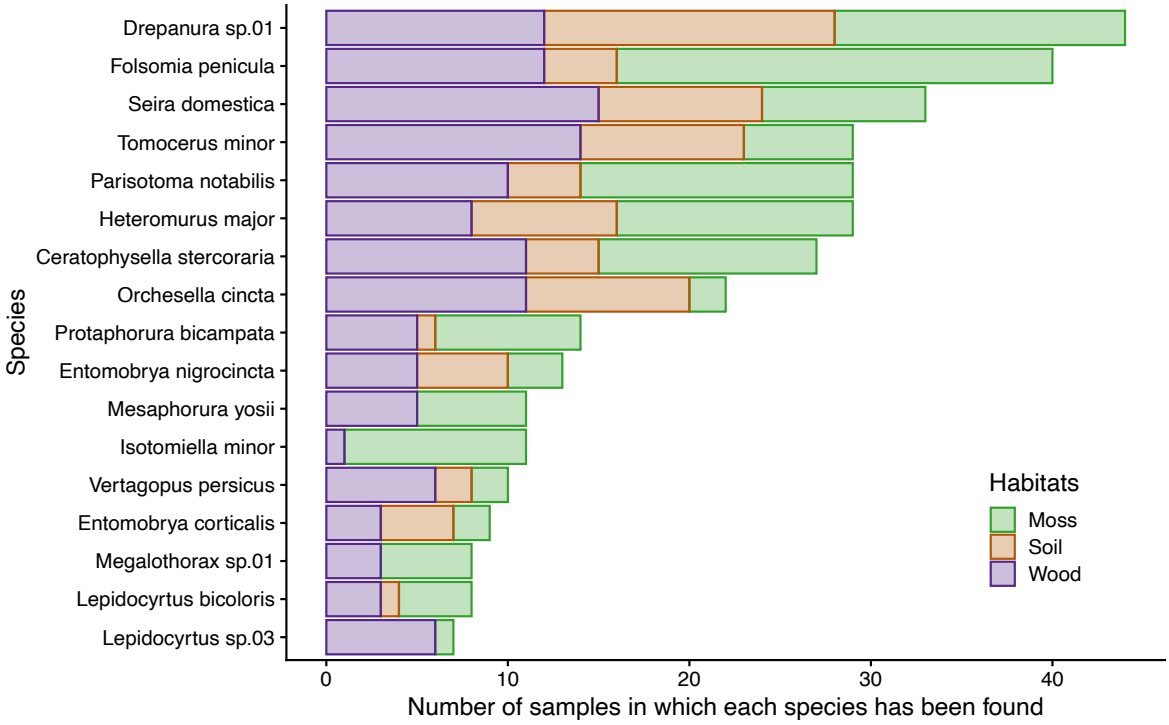

Figure 10 Distribution of the 17 species most frequently found in the three different types of microhabitats.

To further explore the potential covariation of some species, as suggested by the three groups revealed in Figure 8, we extended this data exploration with an analysis of co-occurrences between species (Figure 11). Of the 2628 species pair combinations, 234 pairs could be analysed, of which 205 (87.6%) revealed a random association between species, meaning that the observed number of co-occurrences for these pairs of species was not significantly different from the number of co-occurrences expected by chance (Griffith et al., 2016). In most cases, the presence of one species is not significantly dependent on the presence of another species. However, when co-occurrence does occur, it is predominantly driven by positive interactions. Of the 12.4% of non-random associations, we found 20 positive associations (8.5%) and 9 negative ones (3.8%, Figure 11A). For instance, *Tomocerus minor* is found more often than expected in association with *Orchesella cincta*, and *Folsomia penicula* is rarely observed in association with *Seira domestica* (7 co-occurrences compared to the 14 expected, Figure 11B).

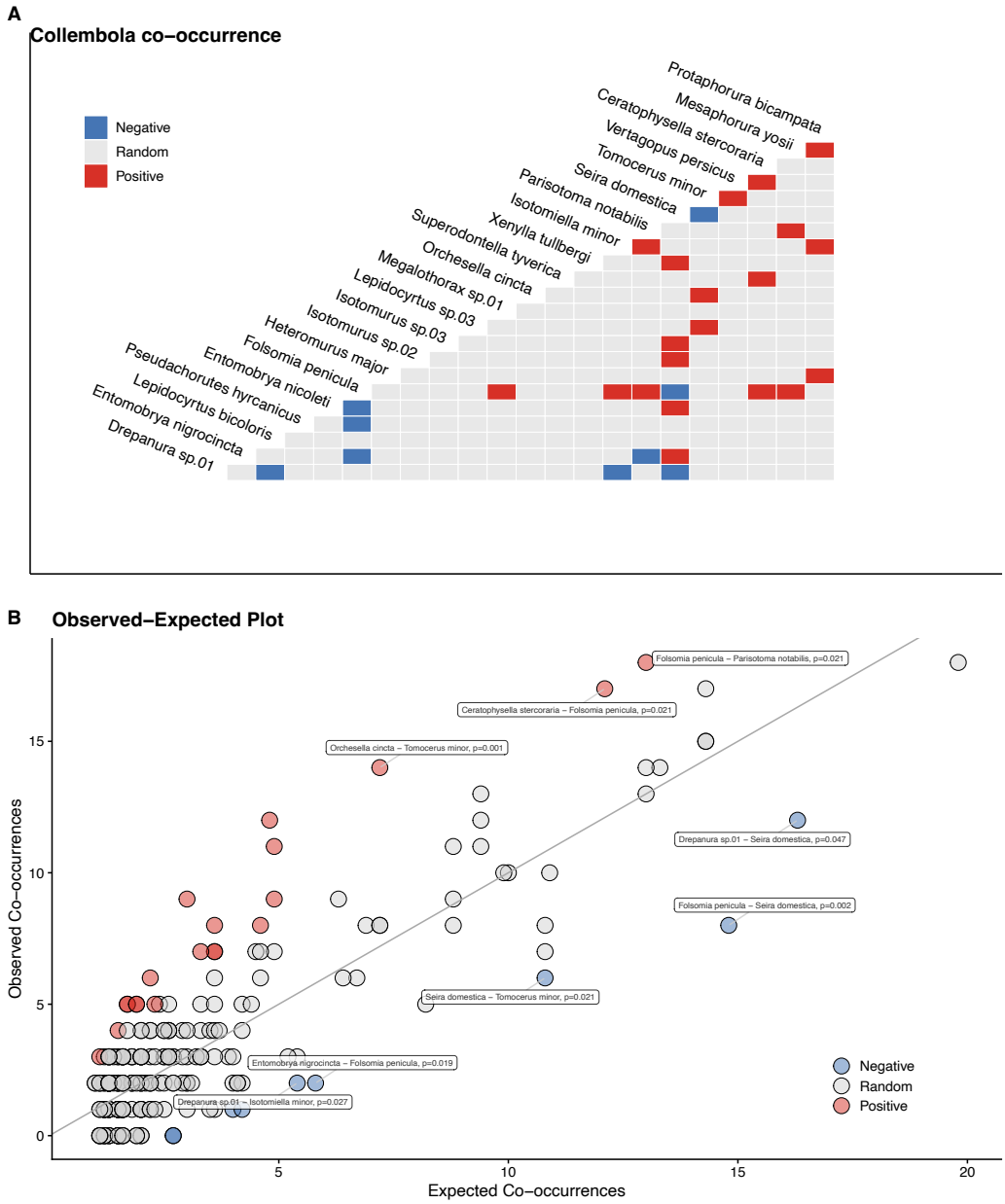

Figure 11 Co-occurrence between species. For most of the species' pairs examined, no specific association was observed (random co-occurrence, grey). Species that are positively associated are underlined in red and those that are negatively associated are underlined in blue.

Discussion

The Bula Forest, part of the ancient Hyrcanian forest and a UNESCO World Heritage Site, represents a rare example of old-growth forest with minimal human disturbance—particularly in its preserved natural sections. This study offers a comprehensive assessment of Collembola communities within this forest massif, focusing on key ecological attributes such as abundance, ubiquity, diversity, richness, and evenness. Sampling took place close to the contact zone of two biodiversity hotspots, across three forest types with contrasting management histories—a preserved planted forest, a preserved natural forest, and a non-preserved natural forest—and within three microhabitats in each site: wood, moss, and soil/leaf litter.

Despite the ecological importance of the Hyrcanian forests, little research has been devoted to the structure and ecological dynamics of Collembola communities. Most previous studies have been limited to faunistic surveys. In the present study, 73 morphospecies were identified, spanning 39 genera and 12 families, with

49 species determined at the species level—highlighting a notably high level of diversity. For comparison, Mehrafrooz Mayvan et al. (2015a) previously reported 20 species across 16 genera and 9 families in the Semeskandeh Forest, including the description of a new endemic genus and species, *Persanura hyrcanica* (Mehrafrooz Mayvan et al., 2015b). In another study from Golestan National Park, 46 Collembola taxa were recorded (Khanahamdi et al., 2018). By 2019, a total of 107 species belonging to 14 families and 51 genera were known from the northern forests of Iran (Shayanmehr and Yahyapour, 2019), some of which, like *Pseudachorutes hyrcanicus*, are endemic (Shayanmehr et al., 2022).

Our sampling protocol enabled robust estimates of local diversity. Species richness per site or habitat ranged from 32 to 52 for observed diversity and from ~40 to over 60 for estimated richness. These values are at the upper end of what is known for temperate forest Collembola communities, where average species richness typically hovers around 38, with 75% of studies reporting fewer than 51 species (Potapov et al., 2023). Overall, estimated total richness in the Bula Forest exceeded 90 species, which is remarkably high for a temperate ecosystem (Potapov et al., 2023; Addison et al., 2003; Sławska et al., 2017; Korboulewsky et al., 2021; Cassagne et al., 2006; Sławski and Sławska, 2020), but comparable to biodiversity levels observed in the central Pyrenees (Lauga-Reyrel and Lauga, 1995), some Canadian (Raymond-Léonard et al., 2020), Caucasus (Kuznetsova et al., 2019) or Chinese forests (Xie et al., 2025), although lower than in some relict forests in Russia (Kuznetsova et al., 2021) and Poland (Smolis and Skarżyński, 2003; Skarzynski and Smolis, 2006). However, methodological differences—particularly in sampling effort, site number, and taxonomic resolution—make direct comparisons difficult.

Importantly, our study expanded the scope beyond traditional soil and litter sampling by including mosses and dead wood, which significantly increased the number of observed species: approximately 55% more species were recorded thanks to these additional microhabitats (26 of the 73 species were found exclusively in moss or wood). This broader habitat coverage likely contributed to the higher diversity observed compared to other recent studies in Iran, such as those in the Zagros oak forests (Shayanmehr and Yahyapour, 2019; Ahmadi et al., 2023).

Nonetheless, our inventory is not exhaustive. Several taxonomic groups—such as Symphypleona and Neelipleona—remain underrepresented, and seasonal limitations (absence of autumn sampling) likely led to the omission of some temporally restricted species. Although our sampling effort had the advantage of being based on two years—which turned out to be relatively similar—it should be remembered that the composition of springtail communities can vary significantly from one year to the next, as shown by an 11-year monitoring of springtail communities in a pine forest in northern Latvia (Dirilgen et al., 2018). Longer term monitoring, over several seasons and years, across wider altitudinal gradients, different valleys and with deeper taxonomic resolution would be required to fully characterise the springtail communities of this forest massif.

The cumulative species curves revealed notable differences in species richness both between microhabitats and across different sites. The divergence of the cumulative species curves between the three microhabitats, and between the three sites, highlight spatial heterogeneity in diversity at two distinct spatial scales. Within sites, our study demonstrates that Collembola diversity is highest in dead wood and lowest in mossy habitats. This pattern is evident at the sample level (Figure 3B) and is further reinforced when comparing the cumulative species curves (Figure 4C). Moreover, this difference between habitats persisted—and even intensified—when the relative abundance of each species was considered (Figure 5B).

Dead wood not only supports a greater abundance and number of Collembola species but also fosters communities with more balanced relative abundances. Similar findings have been reported in Quebec forests, where 74 Collembola species were documented in dead wood microhabitats (Raymond-Léonard et al., 2020). Our results reinforce the view that dead wood in forests serves as a critical habitat for a high diversity of springtails, as well as other taxonomic groups (Skubała and Marzec, 2013). This underscores the importance of conserving various types of dead wood in forests ecosystems, as they provide rich and diverse microhabitats (Seibold et al., 2016) and contribute significantly to habitat heterogeneity (Fujii et al., 2023).

Furthermore, our study shows that the specific diversity of Collembola communities differs on average between the three sites. The site with the highest species richness is the preserved anthropogenic forest, whereas the non-preserved forest exhibits the lowest species richness. However, when considering not only species numbers but also their relative abundance, the preserved natural forest emerges as the most diverse in terms of Collembola communities. Thus, our observations support the importance of preserving natural forests in order to maintain communities that are both species-rich and balanced in terms of relative abundance, aligning with previous studies (Deharveng, 1996; Oliveira and Deharveng, 1995; Susanti et al., 2021).

Nevertheless, this conclusion warrants further investigation, as our study examined only a single site per forest management type, making it difficult to definitively attribute the observed differences to specific management practices. But taking a step back allows us to consolidate this idea: when comparing the diversity of Collembola in the Bula Forest natural area that we studied, which is overall very well protected (UNESCO heritage), with that of less protected Hyrcanian forests subjected to continuous disturbances such as logging, land-use changes, road constructions, and recreational infrastructure development, we observe clear differences: In the well-protected Bula Forest, both Collembola diversity and density are notably higher, with 47 species and 12,400 individuals per square metres on average the soil samples compared to an average of 7600 ind.m^{-2} in the less-protected Semeskaneh Forest (Mehrafrooz Mayvan et al., 2015a). This comparison further emphasizes the vital importance of conservation measures in maintaining high levels of biodiversity in pristine forest ecosystems.

Abundance and ubiquity varied greatly between species. *Seira domestica* was the most abundant species, both locally and globally, and one of the most frequently observed in our different samples in the Bula Forest. This species therefore has all the characteristics of a species that can be described as "common" in our study site (Avolio et al., 2019). It is interesting to note that it is the only one that is common in these communities, while in Semeskandeh Forest (Mehrafrooz Mayvan et al., 2015a; Ghasemi Charati et al., 2021) and in three other Hyrcanian forests, namely Zare, Dohezar and Langar (Yahyapour et al., 2019), *Heteromurus major* was the most abundant species. However, apart from the total number of individuals, which can vary widely due to different population dynamics, our study also found that *Heteromurus major* was one of the most ubiquitous species in our samples.

Comparing the abundance and ubiquity of different springtail species shows that different families contain a few species that are dominant in both number and presence, and other species that are much rarer and less abundant. For example, Figure 7 shows that the dominant species belong to five different families. The Neanuridae family is peculiar in that it includes species that are never frequent, but sometimes locally abundant. Further ecological studies may help to understand the reason for this observation. Such a pattern could be due to strong spatial population structure in the form of locally dense aggregations of individuals, combined with limited dispersal capacity or reduced mobility.

Most common species are generalists. The most common species are generalists in the sense that they can colonize all three types of microhabitats. Some of these species are composed of quite large and mobile specimens (*Depanura sp.*, *S. domestica*, *H. major*, *T. minor*), and it is possible that the territory explored by these individuals may encompass the different types of habitats surveyed. But this is questionable for other smaller species such as *Parisotomia notabilis*. More specialized species, i.e. those that prefer or avoid one of the microhabitats, are also generally less often present in the samples.

Co-occurrence analysis reveals the existence of covariation between certain pairs of species. The co-occurrence study we carried out shows that for most pairs of species the interactions are neutral, in the sense that the presence of one species is not influenced by the presence of another. However, we were able to show the existence of a number of positive interactions between species and a smaller number of negative interactions. The latter could be a sign of interspecific competitive relationships. However, the origin and ecological significance of both positive and negative interactions remain to be elucidated. Experimental approaches in the laboratory could provide a better understanding of the mechanisms by which the abundance of one species can be increased by the presence of another. Is this due to direct or

indirect relationships? We can imagine, for example, that certain species are attracted to the same types of food or to the same types of micro-ecological conditions.

To our knowledge, this type of analysis has rarely been carried out on Collembola. It would be interesting to see if the same type of associations between pairs of species can be observed in other datasets and in other forest ecosystems. The associations we have revealed could also help to select species pairs for experimental studies to better understand the ecological causes of these associations (competition, some sort of exploitation or even mutualism…).

Conclusion

Despite being limited to just three sites within a relatively small portion of the Hyrcanian Forest, and acknowledging that certain Collembola groups remain understudied, our study reveals exceptionally high local Collembola diversity. This richness, observed in forests located at the intersection of two major biodiversity hotspots, underscores the high ecological value of the region. The global significance of this ecosystem is further recognized by its inclusion on the UNESCO World Heritage List. Our findings also reinforce the importance of conserving protected forests, particularly those with abundant deadwood, which provides spatial structure and essential habitats that support species-rich Collembola communities.

Although we did not detect any clear structuring of Collembola communities between sites or habitats, our analyses revealed the positive and negative associations between certain species within the studied communities. This finding opens new avenues for research into the nature of interactions that may shape Collembola assemblages in forest ecosystems.

Authors Contributions

TT, EYL, CDH and MS conceived the ideas and designed the sampling protocol; EYL took the samples in the field, set up the Berlese equipment and sorted the animals. MGS did the soil analysis. MS, CD and EYL identified the specimens. TT and CDH organized the database. TT did the statistical analysis and produced the graphics. TT led the writing of the manuscript. All authors gave final approval for publication.

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