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Windthrow Impact on Alpine Forest Humipedon: Soil Microarthropod Communities and Humus Dynamics Five Years after an Extreme Windstorm Event

Francesca Visentin [1,2], Sara Remelli [1], Augusto Zanella [3] and Cristina Menta [1,*]

[1] Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, 43124 Parma, Italy; francesca.visentin@unifi.it (F.V.); sara.remelli@unipr.it (S.R.)
[2] Department of Biology, University of Florence, 50019 Sesto Fiorentino, Italy
[3] Department of Land, Environment, Agriculture and Forestry, University of Padua, 35020 Legnaro, Italy; augusto.zanella@unipd.it
* Correspondence: cristina.menta@unipr.it

Abstract: The ecological impact of windthrow disturbance on humipedons and soil microarthropod communities is examined in two areas of the Italian Alps (Val di Fassa and Cansiglio) five years after the Vaia Storm. The following soil coverage conditions were identified: herbaceous vegetation (G), decaying wood (W), no vegetation (B) in windthrow areas; and these were compared with conditions in adjacent undisturbed intact forests (IF) and, only in Val di Fassa, with permanent meadows (M). Soil pH, soil organic matter content (SOM), humus systems and microarthropod communities were analyzed. In Val di Fassa, SOM loss was observed in windthrow areas vs. IF, moving toward a Mull humus system, while G evolved toward M-like conditions, W maintained a thicker O horizon and lower pH and B exhibited severe soil erosion and the lowest SOM. In Cansiglio, windthrow areas showed a slower transition to a Mull system, with a trend toward increasing pH and decreasing SOM. A clear relationship between microarthropod communities and humus systems could not be established because the consistency and biological origins of the humus diagnostic horizons were not considered. Microarthropod communities under different conditions exhibited significant dissimilarity, with varying responses across groups; Shannon and QBS-ar indices remained stable except for a significant decrease in B. Community dissimilarity thus appears to be enhanced by post-windthrow disturbance, suggesting that destructive windstorms may also present an opportunity for enriched microarthropod diversity.

Keywords: soil fauna; humipedon; windthrow; humus

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1. Introduction

Over recent decades, anthropogenic climate change has not only caused changes in mean climate variables but has also increased the risk of extreme weather events such as heatwaves, drought, storms and floods [1–3]. Among terrestrial ecosystems, forests are particularly sensitive to these extreme events, because the long lifespan of trees hampers rapid adaptation to sudden environmental change [1]. In particular, wind represents the primary natural disturbance factor impacting forests in Europe, accounting for >50% of tree damage; in fact, each year, an average of two catastrophic windstorm events occur, resulting in a loss of 38,000,000 m^3 of standing timber [4]. A significant increase in forest disturbance has also been confirmed in a recent study by Patacca et al. [5], who estimated an average of 43,800,000 m^3 of disturbed timber per year (most likely an underestimate) in 34 European countries over a 70-year study period.

In October 2018, one of these extreme windstorm events (known as the "Vaia Storm") struck large sectors of the eastern Italian Alps comprising the regions of Lombardia, Veneto, Trentino–Alto Adige and Friuli Venezia Giulia. With wind speeds of up to 200 km h^{-1}, this event caused the loss of nearly 8.3 million cubic meters of timber across 42,500 acres of severely affected forests [6].

It is known that the impact of windthrow on soil can be very severe locally, primarily on account of tree uprooting, which results in the formation of the characteristic pit-and-mound relief. In such sites, local changes in soil chemistry and hydrology occur as a result of plant material deposition, the disruption and redistribution of surface soil organic matter (SOM), the inversion of soil horizons and changes in soil porosity [7–9]. In addition, loss of canopy cover following tree uprooting exposes topsoil layers to solar irradiation, thus increasing both soil temperature and microbial activity [9], resulting in increased CO_2 emissions [10,11]. Consequently, there is a loss of soil organic carbon (C) and a decrease in the soil organic matter C:N ratio [12,13]. Such alterations in the topsoil have a strong impact on the humipedon of damaged forests and are responsible for the characteristic patchy structure of disturbed forest soil ecosystems [14].

The variations caused by windstorms can also influence humus formation dynamics. Humus results from the interplay between mineralogical components, climatic conditions, vegetation and soil biodiversity [15], with its formation strictly linked to animal digestion, which transforms plant residue into an "amorphous" mass that then undergoes decomposition by bacteria and fungi [16]. Variations caused by storms at the micro- and macrohabitat levels influence the structure of soil populations [17,18] and the balance of soil trophic chains, thus affecting the dynamics of humus formation and, consequently, ecosystem stability [19]. In fact, the various humus forms have been acknowledged as dynamic ecological integrating indicators for assessing changes in forest ecosystems, with a response time of years from the disturbance [20].

In Europe, as windthrows are classified as pulse disturbances (together with fires or burrowing) and are an essential part of forest ecosystem dynamics, soil animals have adapted to face the characteristic disturbance regime of the particular ecosystem in which they evolved [21]. Disturbances have also been recognized as a means of enhancing forest regeneration [14]. As a result of climate change, however, forest disturbance damage is set to increase in Europe, with an increase of 229.4% in cubic meters of timber damaged per year predicted for the period 2021–2030 compared with that for 1971–1980 [2]. It is likely that the recovery dynamics and overall resilience of soil animal communities could be significantly altered under such a scenario. The ability to predict the effects of such disturbance in forest humipedon ecosystems is, therefore, of crucial importance in order to develop new, more effective forest management and conservation practices [22].

Only a few studies have been carried out that focus on the impact of severe windthrow events on humus dynamics and soil living communities. Among these, Lüscher [13] observed that following the passage of Storm Vivian in Switzerland, humus exhibited a transition toward forms characterized by an acceleration of biological activity, organic matter turnover and mixing with the mineral fraction. Regarding soil fauna, the literature has focused on either a single taxon or a small group of taxa of microarthropods, notably Acarina and Collembola [17,23,24], with results that are not always consistent with each other. In a study focused on the effects of the Vaia Storm on the soil microarthropod community one year after the disturbance, Menta et al. [25] found that not all taxonomic groups reacted in the same way to the windthrow. On the other hand, the study by Sterzyńska et al. [26] revealed that soil biogeochemistry and resource availability had a greater influence on the distribution and abundance of Protura assemblages than forest disturbances.

As far as we can ascertain, no study has yet investigated the combined response of soil microarthropod communities and humus systems to extreme windstorm disturbances. Therefore, our study investigates the effects of the Vaia Storm with the specific aims of (i) characterizing the different habitats created in forests as a result of windthrows; (ii) identifying how the type of humus in these areas changes in relation to soil coverage conditions resulting from the passage of the storm; (iii) understanding whether some groups of soil microarthropods can be considered indicators of habitat change; and (iv) ascertaining whether there is a link between the arthropod community and the type of humus formed as a result of the catastrophic event. We hypothesized that the spatial heterogeneity resulting from an extreme weather event, such as a severe windstorm, could be an important driver in differentiating microhabitats in damaged forests, with a consequent increase in edaphic biodiversity—an assumption partly neglected in previously mentioned research. Two areas affected by the passage of the Vaia Storm were selected for our study, with results relating to humus type and soil arthropods compared between the two sites.

2. Materials and Methods

2.1. Study Sites

The study was conducted in July 2023, 5 years after the Vaia Storm disturbance. Forests belonging to two different municipalities of the north-eastern Italian Alps were selected: San Giovanni di Fassa, located in Val di Fassa (Trentino-Alto Adige region), and Tambre, located in Cansiglio (Veneto region).

In San Giovanni di Fassa, the geological substrate consists mainly of dolomite limestone. Samplings took place at an altitude ranging from 1600 to 2000 m a.s.l., with the vegetation consisting of a managed forest of spruce (*Picea abies* (L.) H. Karst.) and larch (*Larix decidua* Mill.). In Cansiglio, the geological substrate is also formed of limestone, with the forest being located on a karst plateau, between 900 and 1200 m a.s.l., surrounded by rocky peaks situated in the Italian Prealps. As a result of this geological conformation, cold air is trapped on the plateau, leading to a characteristic thermal inversion. In relation to this temperature gradient, the vegetation consists of a managed spruce forest on the plateau which, as the altitude increases, is gradually replaced by a managed beech forest (*Fagus sylvatica* L.). Samplings took place in both the spruce forest and the mixed spruce-beech forest.

According to the Köppen-Geiger classification, the climate of both areas is categorized as warm-summer humid continental (Dfb); the average annual temperature in San Giovanni di Fassa is 2.4 °C, and the annual precipitation is c. 1885 mm; the mean annual temperature in Cansiglio is 6.1 °C, and the annual mean precipitation is 2049 mm.

2.2. Experimental Design

During the summer of 2023, a total of 23 sites were identified in the two sampling areas (15 in Val di Fassa and 8 in Cansiglio), representing undisturbed vs. disturbed conditions where several windthrow-damaged patches were present following the Vaia Storm (Figure 1a,b). With regard to windthrow sites (6 in Val di Fassa and 4 in Cansiglio), three main soil coverage conditions were identified for evaluating the impact of the windstorm: windthrow areas with herbaceous vegetation cover (grass; G), windthrow areas with decaying wood on soil (W) and windthrow areas characterized by bare soil (B). It is important to note that these conditions were not present in all of the selected sites (see details below). Data gathered from these areas were compared with those collected from undisturbed sites (9 in Val di Fassa and 4 in Cansiglio). In particular, one main undisturbed soil coverage condition was identified, i.e., intact forest adjacent to windthrow areas (IF), with 6 IF sites in Val di Fassa and 4 IF sites in Cansiglio. The final 3 sites were located exclusively in Val di Fassa, which were selected as representatives of permanent meadow (M) in order to test the hypothesis that humus types and microarthropod communities of G areas could be shifting toward those found in permanent meadows in the same area.

All 12 forest sites in Val di Fassa were characterized by a mixed spruce-dominated coniferous forest, whereas half of the sites in Cansiglio consisted of spruce forest and the other half consisting of mixed forest, with beech and spruce being the dominant tree species.

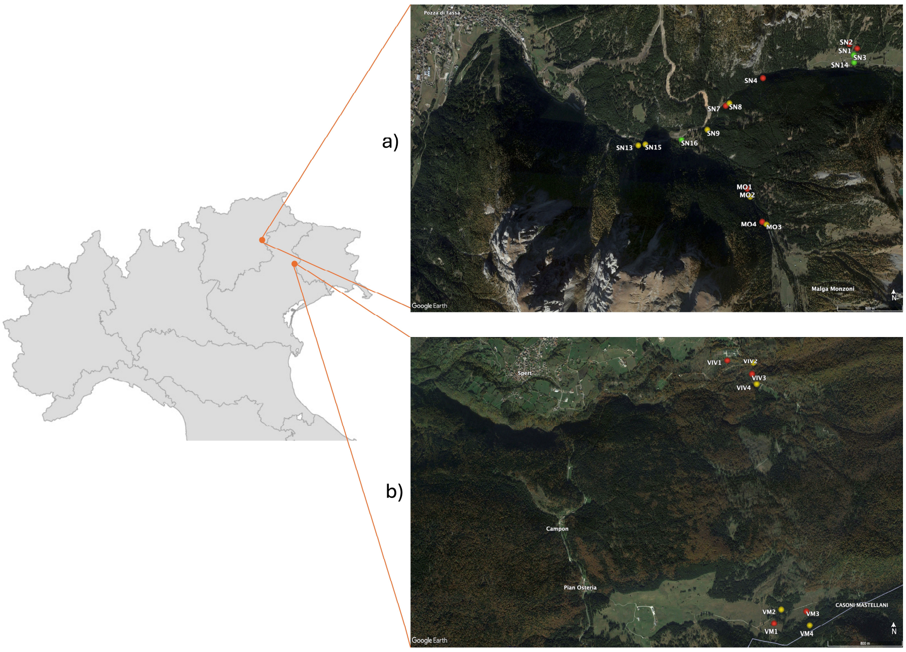

Figure 1. Location of sampling sites in the (**a**) Val di Fassa and (**b**) Cansiglio areas. Yellow dots: intact forest; red dots: windthrow areas; green dots: meadows.

For each soil coverage condition, the following parameters were considered: (1) soil features (pH, soil organic matter content); (2) humus characteristics; (3) soil respiration (CO_2 emission); and (4) soil microarthropod communities. In order to collect data for these parameters, at each sampling site and for each soil coverage condition (when present), three replicate locations were selected that were at least 10 m apart to avoid spatial autocorrelation. For each replicate, after having registered the slope of the soil, the soil respiration was first measured. One soil sample with surface dimensions of 10 × 10 cm and a depth of 15 cm from the soil surface (including the litter layer) was collected for microarthropod extraction. Then, a soil profile was opened in order to identify the soil horizons and to classify the humus system. Finally, within the thickness of each soil horizon, a soil core was taken for chemical analysis.

All soil samples were taken to the laboratory within 72 h. A total of 87 samples were analyzed. For the Val di Fassa study site, 60 samples were gathered with the following distribution: 18 IF, 18 G, 12 W, 3 B and 9 M. In the Cansiglio forest, 27 samples were collected, distributed as follows: 12 IF, 12 G and 3 W.

As already mentioned above, we encountered some difficulty in finding the different soil coverage types with the same frequency within each selected area, which explains the numerical differences in the samples for each condition. For example, bare soil was underrepresented because of vegetation development in the windthrow areas. Despite this, we decided to go ahead with our evaluation of these conditions as even partial results on this extreme condition may be of interest. Furthermore, since there were only two soil coverage conditions found in windthrow sites in Cansiglio (G and W, with W consisting only of 3 replicates), only two conditions were considered for statistical analysis for this area: intact Forest (IF) and windthrow (Wt).

2.3. Soil Features

For each replicate, after measuring the thickness of the O and A horizons, one cylindric soil core of each horizon (of approximately 100 cm^3) was collected for chemical analysis.

Once in the laboratory, each soil core was homogenized and sieved at 2 mm. Subsequently, the pH was measured by placing a pH meter in a soil–distilled water solution at a ratio of 1:5 volume [27]. The soil organic matter (SOM) content was determined by the loss on ignition, putting 6 g of soil (pre-dried in oven at 150 °C) in a muffle furnace at 160 °C for 6 h and then at 400 °C for 4 h [28]. The SOM content (hereafter, simply SOM) was then calculated according to the following formula:

$$SOM\% = [(Weight_{160\,^\circ C} - Weight_{400\,^\circ C})/Weight_{105\,^\circ C}] \times 100$$

2.4. Humus Characterization

A soil profile was opened for humus classification according to Zanella et al. [29]. The profile was opened until the maximum depth of the A horizon; the thickness of all diagnostic horizons found in each profile (OL, OF, OH and A) was recorded. The humus system was classified based on the qualitative characteristics and thickness of the diagnostic horizons, as well as on the transitions between them.

2.5. Soil Respiration

The soil CO_2 flux was measured using an EGM-5 portable CO_2 gas analyzer (PP Systems, Amesbury, MA, USA) equipped with an SRC-2 soil respiration chamber (1170 cm^3 volume). Before placing the chamber on top of the soil, any fresh litter was removed, and, if present, any grass was cut to 2 cm; a temperature and moisture sensor, connected to the gas analyzer, was placed in the soil next to the chamber. The respiration rate (expressed in $g(CO_2)\ m^{-2}\ h^{-1}$) was calculated by measuring the concentration of CO_2 every second after 60 s.

2.6. Soil Microarthropod Extraction

Soil microarthropods were extracted using an Ecotech Kempson extractor (ecoTech Umwelt-Messsysteme GmbH, 53121 Bonn, Germany) (extraction time: 10 days; maximum extraction temperature: 55 °C) and collected in a container with a preservative solution (ethyl alcohol:glycerol in a ratio of 3:1). The extracted specimens were observed under a stereomicroscope for taxonomic identification at different levels: the class level for Myriapoda and the order level for Hexapoda, Chelicerata and Crustacea. For mites, two groups, Oribatida and Acarina, were considered on account of the close association between Oribatida and soil organic matter. With regard to holometabolous insects, the larvae of Coleoptera, Diptera and Lepidoptera were considered as separate groups as they occupy different niches compared with their adult form. Specimens were then counted to estimate the abundance of each group and the total abundance of microarthropods (expressed as individuals/m^2) in the first 15 cm of the topsoil. For each soil sample, the microarthropod community was analyzed in terms of group richness and diversity using the Shannon diversity index. The QBS-ar index (a soil biological quality index based on soil arthropods) was also applied [30].

2.7. Data Analysis

R software v 4.4.0 was used for all the analyses. For the purpose of statistics, for each replicate, a single value was calculated for each soil chemical parameter (pH and SOM) representing the mean value for the O and A horizons within the first 15 cm of soil (i.e., the depth of the soil sample taken for microarthropod extraction). The calculation was performed as a weighted mean, considering the relative thicknesses of the O and A horizons within the top 15 cm of the soil.

A factor analysis of mixed data (FAMD) (package: FactoMineR) was carried out on the complete dataset to capture the relationships between the variables and to determine how these are distributed in the principal component space. The variables used for this analysis were both quantitative (A thickness, O thickness, slope, pH, SOM, Shannon index, QBS-ar, arthropod density and number of groups) and qualitative (sampling areas, humus system and soil coverage conditions). On the basis of the results obtained, we decided to analyze the two sampling areas separately, and FAMD was re-performed on each area (Val di Fassa and Cansiglio). ANOVA assumptions were tested (package: stats) and, as these were not met, non-parametric tests were applied instead (package: stats). The subsequent analyses were conducted on each area. Spearman's correlation (package: stats) was used to evaluate the relationship between all the quantitative variables related to the physical-chemical and biological parameters considered in this study.

Generalized linear model (GLM) tests (package: stats) were used, selecting all the following quantitative parameters as response variables: SOM, pH, total groups, total individuals, Shannon, QBS-ar and CO_2. Depending on the variable, either the Poisson family (or quasi-Poisson if there was data overdispersion) or the Gaussian family was used. After selecting the model with the lowest AIC, only models showing significant predictors were reported. Where qualitative variables were significant, Dunn's test was applied (package: FSA).

For the community structure analysis, PERMANOVA (package: vegan) was performed first to test the hypothesis that there are significant differences among the main categorical variables (area, condition, vegetation and humus system) in a multivariate analysis context using a dissimilarity matrix as input (in this case, Bray-Curtis). To reduce the impact of outliers and the effect of overestimation, community data was first square-root-transformed. On the basis of the PERMANOVA results, it was decided to also treat the two areas separately in this case, and SIMPER (Similarity Percentage) was therefore applied (package: vegan). This method provides an assessment of the percentage dissimilarity based on the composition of arthropod groups and also evaluates the relative importance of each group's contribution to the sample dissimilarity.

For the analysis of the association between taxa and sites, multilevel pattern analysis was used (package: indicspecies). The functions "r.g" and "IndVal.rg" were both utilized, with the former ("Relative Abundance—Gradient") used to evaluate the association between the relative distribution of a taxon and an environmental variable.

Overall, a p-value < 0.05 was considered significant.

3. Results

FAMD was applied in order to examine the quantitative and qualitative variables collectively. The analysis identified a pattern that suggested a distinction between the Val di Fassa data and those from Cansiglio, with these two areas clustering in opposite dimensions on the graph (see Figure S1 in Supplementary Materials). Consequently, statistical analysis was carried out separately for the two study areas. As the chemical parameters did not show the same variation trend, both areas were therefore analyzed together.

3.1. Chemical Analysis

The pH of the top 15 cm of soil in both areas was found to be acidic or very acidic under all soil coverage conditions (mean and standard error: 5.62 ± 0.73). IF had the most acidic condition (5.21 ± 0.61) when compared with G and M (Figure 2a). Additionally, IF showed the highest SOM content ($39.28 \pm 21.38\%$), which was higher than in both G and M (Figure 2b).

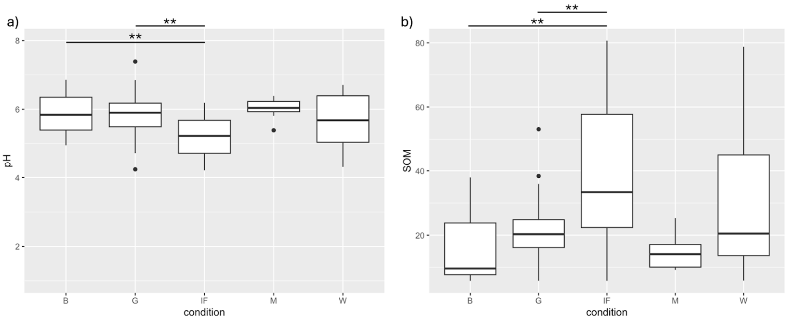

Figure 2. Boxplot of the (**a**) pH and (**b**) soil organic matter (SOM; %) in the topsoil (15 cm) of each soil coverage condition in both sampling areas. B = bare soil in windthrow areas; G = under grass in windthrow areas; IF = intact forest; M = permanent meadow; W = under decaying wood in windthrow areas. ** = $p < 0.01$.

3.2. Humus Characterization

In Val di Fassa, almost all sampling replicates (88%) exhibited an Amphi humus system in IF, whereas in all the other soil coverage conditions, at least 50% of the samples were characterized by a Mull humus system (Table 1).

Table 1. Soil features, horizon thickness, and humus systems found in the two sampling areas for each soil condition (mean ± standard error). IF = intact forest; M = permanent meadows; G = under grass in windthrow areas; W = under wood in windthrow areas; B = bare soil in windthrow areas; Wt = windthrow. Humus system horizons: Mull (A horizon); Amphi and Moder (O + A horizons); Tangel (O horizon).

		pH	SOM (%)	Thickness O (cm)	Thickness A (cm)	Humus System (%) Mull	Amphi	Moder	Tangel
Val Di Fassa	IF	5.34 ± 0.13	43.18 ± 5.91	10.03 ± 2.27	6.92 ± 1.09	0	83.3	16.7	0
	M	5.59 ± 0.10	21.12 ± 1.94	3.73 ± 0.52	11.55 ± 0.52	66.7	33.3	0	0
	G	5.88 ± 0.15	19.42 ± 1.98	3.86 ± 0.90	11.53 ± 0.97	55.6	44.4	0	0
	W	5.59 ± 0.25	29.95 ± 6.35	7.92 ± 1.44	9.25 ± 1.84	50	41.7	0	8.3
	B	5.88 ± 0.55	17.78 ± 10.13	0.33 ± 0.33	14.67 ± 0.33	66.7	33.3	0	0
Cansiglio	IF	5.01 ± 0.19	33.43 ± 3.79	6.42 ± 0.92	9.08 ± 1.12	8.3	91.7	0	0
	Wt	5.86 ± 0.19	26.85 ±3.70	4.27 ± 1.38	11.87 ± 1.24	33.3	60	0	6.7

In Cansiglio, the findings were similar to those in Val di Fassa. An Amphi humus system was predominant in IF, whereas in windthrow areas, a shift toward the Mull system was present, but this was less pronounced than that observed in Val di Fassa. Within G, the Mull system accounted for 33.33% of the observations; in W, the greatest variability was found (Table 1).

3.3. Microarthropod Parameters and Soil Feature Associations

3.3.1. Val Di Fassa

In Val di Fassa, IF exhibited the lowest pH mean value and the highest mean SOM (Table 1). The thickness of both the O and A horizons reflected this trend, with IF having the thickest O horizon and the thinnest A horizon (Table 1).

Soil respiration (g(CO_2) m^{-2} h^{-1}) was highest in M followed by IF and G (2.25 ± 0.41, 2.02 ± 0.38 and 1.98 ± 0.25, respectively), showing a strong decrease in both W and B (1.32 ± 0.22 and 1.18 ± 0.09, respectively).

A total of 13,753 specimens of microarthropods were extracted from all the samples collected in Val di Fassa, with the abundance ranging between 27,204.96 ind/m^2 in a sample of the G condition and 28.88 ind/m^2 in a sample of the B condition (all the abundance data are presented in Supplementary Materials). The total number of groups and the total abundance of microarthropods showed a declining trend in W, with a more pronounced decline observed in B (Figure 3a,b). The Shannon diversity index and the QBS-ar index showed a decrease only in B (Figure 3c,d).

Two clusters of qualitative variables in the different dimensions of the FAMD graph could be observed in Figure 4, with M and G and the Mull humus system grouped together, and Mull correlated with the thickness of the A horizon and pH. On the opposite side of the graph, IF and W are grouped together with the Amphi humus system. These variables correlated with the SOM and the thickness of the O horizon. The soil coverage condition B diverged from all the others, appearing to be negatively associated with all the soil arthropod variables and soil respiration. The slope of the site had relatively little importance in contributing to the principal components. Regarding humus systems, the Moder and Tangel cluster diverged from the rest of the humus systems, correlating positively with the SOM and the thickness of the O horizon.

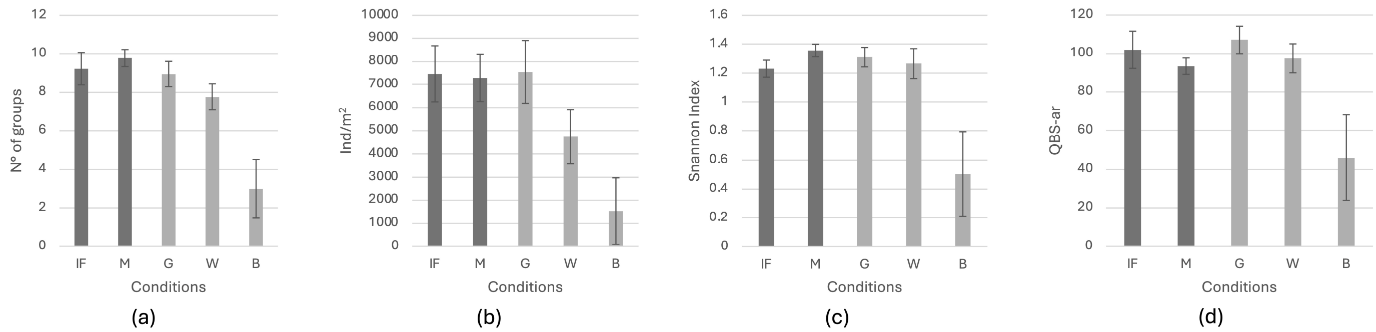

Figure 3. Histograms representing the mean and standard error of the (**a**) number of microarthropod groups, (**b**) number of specimens per square meter (total abundance), (**c**) Shannon diversity index, and (**d**) QBS-ar index for each soil coverage condition in Val di Fassa. IF = intact forest; M = permanent meadow; G = under grass in windthrow areas; W = under decaying wood in windthrow areas; B = bare soil in windthrow areas.

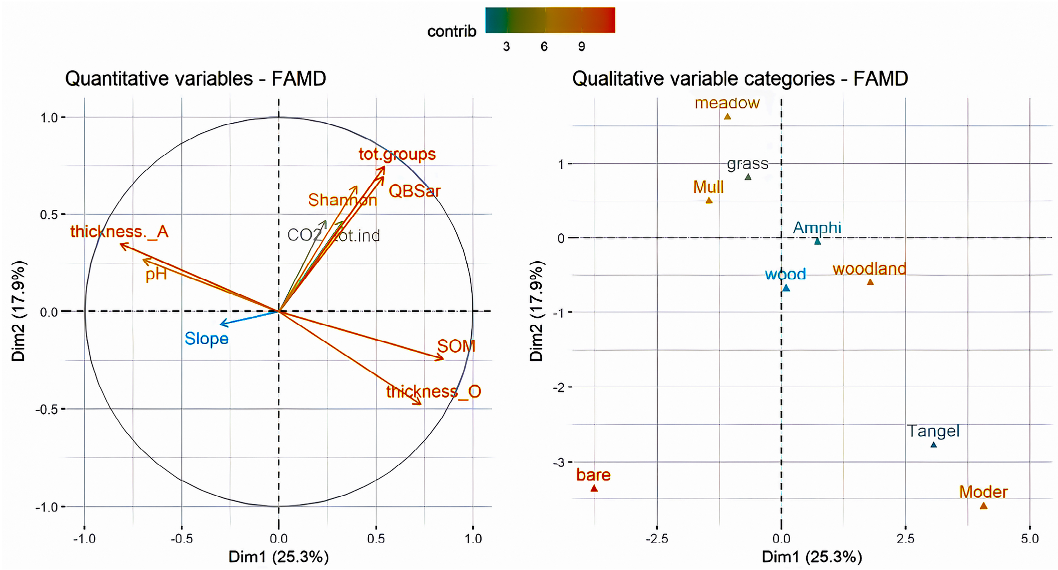

Figure 4. FAMD graph representing all the quantitative and qualitative variables from the Val di Fassa area.

Several of the relations between variables that emerged from FAMD analysis were confirmed by Spearman correlation, as presented in Figure 5a.

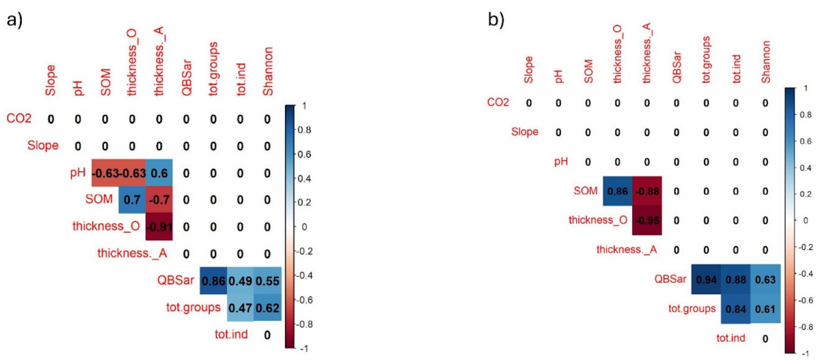

Figure 5. Spearman correlation output between the quantitative parameters in (**a**) Val di Fassa and (**b**) Cansiglio. Numbers indicate the positive or negative correlation coefficient.

GLM analysis (see Table S1 in Supplementary Materials) showed that the soil coverage condition, rather than the humus system, had a significant impact on the number of taxonomic groups, the Shannon index and the QBS-ar index. Pairwise comparisons revealed that B and M were significantly different ($p < 0.05$) in both the number of groups and the Shannon index, with B showing lower values for all indices.

Soil respiration was influenced by the soil coverage condition, SOM and the humus system, with significant differences between B and M ($p < 0.01$) and B and G ($p < 0.05$), which indicated lower CO_2 emissions in B. Finally, SOM was influenced by the humus system, with significant differences between Mull and Amphi ($p < 0.01$) and between Mull and Moder ($p < 0.05$) indicating a lower SOM in Mull in both cases.

The structure of the microarthropod community in Val di Fassa was affected both by the soil coverage condition ($p = 0.001$) and pH ($p < 0.05$) but not by the humus system. Pairwise comparisons indicated that the two conditions with communities significantly different from the others were W ($p < 0.05$ for all comparisons) and B ($p < 0.005$ compared with IF; $p < 0.01$ for all other comparisons). The community in B differed by 71.6% from that in M; the communities in B and IF differed by 69.1%; those in B and G, by 68.9%; and both those in W and IF and those in W and G, by 41.7%. The main microarthropod groups determining the dissimilarity between conditions are listed in Table 2. The microarthropod groups statistically associated with a particular soil coverage condition were the larvae of Coleoptera for M ($p < 0.01$) and non-Oribatida for the group of conditions G + M + IF ($p < 0.05$).

Table 2. Cumulative dissimilarity explained by each microarthropod group for the compared soil coverage conditions. For Val di Fassa, the abundance data are reported for the first and the second term of the comparison. IF = intact forest; M = permanent meadow; G = under grass in windthrow areas; W = under decaying wood in windthrow areas; B = bare soil in windthrow areas; Wt = windthrow area. Results are reported for each study area: VdF = Val di Fassa; Can = Cansiglio.

Area	Comparison	SIMPER Coefficient	Group	Cumulative Dissimilarity Explained	Ind/m^2 First Condition (Mean ± St. Error)	Ind/m^2 Second Condition (Mean ± St. Error)
VdF	B vs. M	0.716	Collembola	0.249	211.79 ± 197.52	2987.48 ± 645.39
			Non-Oribatida	0.458	981.92 ± 910.06	2679.42 ± 375.55
			Oribatida	0.599	298.43 ± 298.43	834.31 ± 152.04
			Coleoptera-Lavae	0.680	0	173.28 ± 20.15
			Symphyla	0.742	9.63 ± 9.63	253.50 ± 96.23
	B vs. G	0.689	Non-Oribatida	0.263	981.92 ± 910.06	3411.05 ± 560.50
			Collembola	0.468	211.79 ± 197.52	1846.72 ± 326.59
			Oribatida	0.654	298.43 ± 298.43	1565.94 ± 531.89
			Protura	0.706	0	190.93 ± 116.67
	B vs. IF	0.691	Collembola	0.240	211.79 ± 197.52	2486.89 ± 589.42
			Non-Oribatida	0.472	981.92 ± 910.06	2613.64 ± 402.34
			Oribatida	0.668	298.43 ± 298.43	1702.32 ± 494.76
			Hemiptera	0.720	0	120.33 ± 39.98
	B vs. W	0.677	Collembola	0.281	211.79 ± 197.52	2596.79 ± 886.71
			Non-Oribatida	0.493	981.92 ± 910.06	1280.35 ± 313.24
			Oribatida	0.671	298.43 ± 298.43	527.06 ± 82.16
			Coleoptera-larvae	0.734	0	72.20 ± 16.48
	W vs. G	0.417	Collembola	0.222	2596.79 ± 886.71	1846.72 ± 326.59
			Non-Oribatida	0.416	1280.35 ± 313.24	3411.05 ± 560.50
			Oribatida	0.549	527.06 ± 82.16	1565.94 ± 531.89
			Protura	0.609	7.22 ± 3.77	190.93 ± 116.67
			Pauropoda	0.665	40.91 ± 16.85	123.54 ± 42.01
			Symphyla	0.718	45.73 ± 17.22	105.89 ± 41.96

Table 2. *Cont.*

Area	Comparison	SIMPER Coefficient	Group	Cumulative Dissimilarity Explained	Ind/m^2 First Condition (Mean ± St. Error)	Ind/m^2 Second Condition (Mean ± St. Error)
	W vs. IF	0.417	Collembola	0.234	2596.79 ± 886.71	2486.89 ± 589.42
			Non-Oribatida	0.399	1280.35 ± 313.24	2613.64 ± 402.34
			Oribatida	0.544	527.06 ± 82.16	1702.32 ± 494.76
			Hemiptera	0.603	2.41 ± 2.41	120.33 ± 39.98
			Diplopoda	0.653	67.39 ± 20.21	48.13 ± 26.62
			Pauropoda	0.700	40.91 ± 16.86	73.80 ± 21.43
Area	**Comparison**	**SIMPER coefficient**	**Group**	**Cumulative dissimilarity explained**	**Ind/m^2 IF (mean ± st.error)**	**Ind/m^2 Wt (mean ± st.error)**
Can	IF vs. Wt Conifers	0.468	Non-Oribatida	0.155	1631.72 ± 640.19	2113.05 ± 398.25
			Collembola	0.292	948.23 ± 495.09	1010.8 ± 206.51
			Symphyla	0.414	173.28 ± 98.64	644.99 ± 265.49
			Oribatida	0.514	827.89 ± 513.04	601.67 ± 228.31
			Hemiptera	0.588	67.39 ± 33.90	423.57 ± 406.29
			Coleoptera—larvae	0.652	255.11 ± 89.30	182.91 ± 50.08
			Diplopoda	0.692	77.01 ± 26.54	19.25 ± 14.28
			Pauropoda	0.729	28.88 ± 28.88	52.95 ± 25.19
	IF vs. Wt Deciduous	0.413	Non-Oribatida	0.169	5318.73 ± 1000.03	1992.72 ± 658.58
			Protura	0.298	1044.49 ± 438.77	1273.92 ± 1002.49
			Oribatida	0.411	2098.61 ± 561.43	523.05 ± 156.08
			Collembola	0.508	2223.76 ± 201.88	1870.78 ± 556.37
			Coleoptera—larvae	0.566	192.53 ± 41.96	644.99 ± 521.48
			Symphyla	0.619	524.65 ± 187.52	231.04 ± 55.30
			Pauropoda	0.672	505.4 ± 327.23	170.07 ± 93.26
			Diplopoda	0.714	125.15 ± 39.92	407.53 ± 232.96

3.3.2. Cansiglio

In Cansiglio windthrow areas, a rise in pH and a decrease in SOM were detected. The lower SOM corresponded to a reduction in the thickness of the O horizon and a subsequent increase in the thickness of the A horizon in the top 15 cm of the soil (Table 1).

A total number of 7027 specimens were extracted from the 27 samples, with densities ranging from a minimum of 28.88 ind/m^2 found in an IF sample to a maximum of 24,172.56 ind/m^2 in found in a Wt sample (all the abundance data are presented in Supplementary Materials).

Despite the fact that neither the soil coverage condition nor the humus system was significant in predicting microarthropod parameters, there was a consistent tendency toward lower values in Wt compared to IF for the following variables (Figure 6a–d): total number of groups, total abundance, QBS-ar index and, to a lesser extent, the Shannon index. Similarly, soil respiration (g(CO_2) m^{-2} h^{-1}) also exhibited a consistent decrease in Wt (1.85 ± 0.15) compared to with IF (2.70 ± 0.48).

Positive correlations between all the microarthropod parameters and between the SOM and thickness of the O horizon were observed. Negative correlations were observed between the thickness of the A horizon and both the SOM and the thickness of the O horizon (Figure 5b).

In Cansiglio, pH was significantly influenced by windthrow, the Mull humus system and SOM. Higher values were found in windthrow areas and in Mull, whereas lower values were found in topsoil with a higher SOM. Similarly, soil respiration was also significantly influenced by windthrow, but only in sites characterized by deciduous vegetation, which had lower CO_2 emissions in windthrow areas. The SOM was significantly influenced by both pH and the humus system, with a significant difference between the Mull and Amphi humus systems ($p < 0.05$), indicating a lower SOM in Mull (for GLM results, see Table S1 of Supplementary Materials).

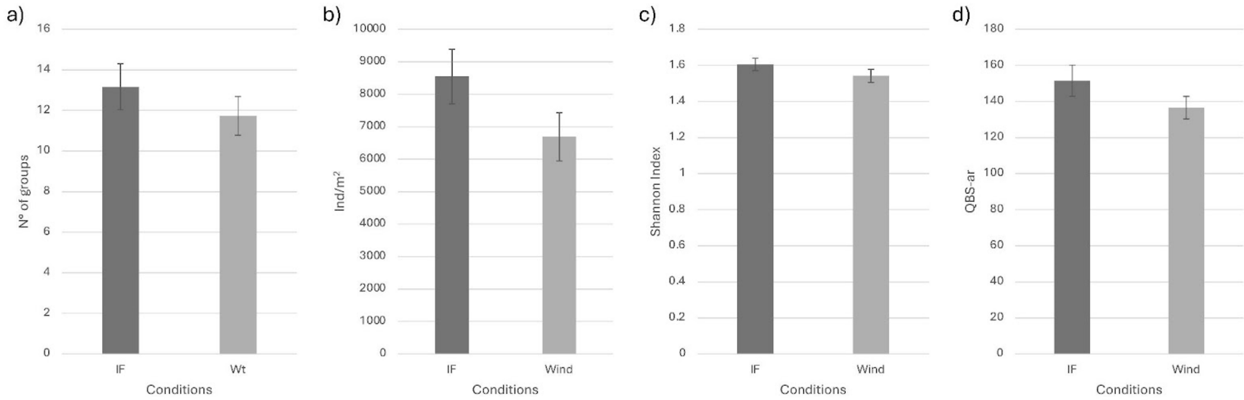

Figure 6. Histograms representing the mean and standard error of the (**a**) number of microarthropod groups; (**b**) number of specimens per square meter; (**c**) Shannon diversity index; and (**d**) QBS-ar index for each soil coverage condition in Cansiglio. IF = intact forest; Wt = windthrow area.

The structure of the microarthropod community in Cansiglio was only affected by vegetation type, i.e., whether coniferous or deciduous ($p < 0.01$), and by the interaction between the vegetation type and the soil coverage condition ($p < 0.05$). Community structure was not influenced by the soil coverage condition alone or by the humus system. Pairwise comparisons revealed significant differences between communities under coniferous IF and deciduous IF ($p < 0.05$) and between IF and Wt under deciduous vegetation ($p < 0.05$).

In detail, the dissimilarity between communities under the coniferous IF and the deciduous IF amounted to 49.3%; between communities under deciduous vegetation in IF and Wt, it amounted to 41.3%. Although pairwise comparison between communities in IF and Wt under coniferous vegetation was not significant, the dissimilarity was 46.8%, an amount comparable with previous dissimilarities. The most important microarthropod groups driving the dissimilarity between IF and Wt under both coniferous and deciduous vegetation are listed in Table 2.

Microarthropod groups statistically associated with the soil coverage condition were only found for IF, namely Oribatid mites and Isopoda ($p < 0.05$ for both).

4. Discussion

Humus systems in both Val di Fassa and Cansiglio soils were found to be in line with the established literature on humus systems typically found on base-rich carbonate or siliceous substrates, as described by Zanella et al. [16]. Specifically, in those sites where windthrow had not affected the forest (i.e., intact forest, IF), the Amphi humus system predominated, which is indicative of forest ecosystems where contrasting ecological conditions—cold winters marked by prolonged biological inactivity followed by warm, ecologically favorable summers—prevail. This particular humus system is characterized by an acidic pH (with average values ≥ 5) and medium-fast SOM turnover. Two Moder humus systems, typical of European forests on acidic bedrock, were also identified in subsites characterized by a podzol, which were characterized by a more acidic pH and an understorey dominated by acidophilic species belonging to the genus *Vaccinium*. In contrast, in sites representing permanent meadows (M) in Val di Fassa, the pH was higher, and the predominant humus system was Mull, with Amphi forms present in almost one-third of the subsites. The thin O horizon in these Amphi forms suggests stronger biological activity and faster SOM turnover compared with the Amphi forms found in forested sites [31–33].

With regard to windthrow-affected soils in Val di Fassa, several distinct trends were observed. Soils under herbaceous vegetation cover (G) tended to evolve toward conditions found in permanent meadows and, compared with intact forest, were characterized by higher pH and thinner O horizons, probably indicating that the humus is still evolving toward a Mull system [34,35]. Soils under decaying wood (W), on the other hand, were more similar to intact forest, with low pH and thicker O horizons. In both Val di Fassa and in Cansiglio, the presence of a Tangel system, which is indicative of strict ecological conditions such as limited sunlight and recalcitrant SOM, was exclusively observed in areas where the soil was covered with decaying wood. Finally, regarding bare soils (B), these represent an extreme condition where surface horizons had been removed by the storm, resulting in the thinnest O horizon and the lowest SOM of all the soil types analyzed in the current study. It is worth noting that the pH in Val di Fassa sites was negatively correlated with O horizon thickness—a correlation that may be attributed to the acidity of undecomposed conifer litter, which constitutes the superficial O horizon in these forested sites [36].

As reported by Schulze et al. [37] and Trumbore et al. [38], the rate of topsoil SOM turnover increases with increasing depth and is also positively correlated with temperature. It is therefore possible that, in our study, the progressive shift from Amphi to Mull humus systems is mainly driven by canopy loss and the subsequent increase in both solar irradiation and temperature in windthrow areas with herbaceous vegetation cover—a shift that has not been observed in windthrow areas under decaying wood due to the thicker soil coverage provided by the timber lying on the ground. Such a hypothesis is further supported by the higher CO_2 flux observed in the areas with herbaceous vegetation cover, which may be attributed to increased temperatures [11]. In contrast, in soils covered by decaying wood, lower CO_2 emissions were recorded, which is probably due to reduced solar irradiation, with the lowest soil respiration detected in bare soils—a result corroborating previous studies [10,39].

In Cansiglio there was a less pronounced shift in windthrow sites (Wt) toward a Mull system than in Val di Fassa. However, the soil feature analysis indicated a trend toward increasing pH, decreasing SOM, a reduction in O horizon thickness and an increase in A horizon thickness compared with intact forest sites. These changes suggest that while the humus system is evolving more slowly, the chemical properties of the soil are changing more rapidly. This is in line with Moscatelli et al. [20], who recognized the role of humus systems as ecological indicators while underlining the fact that response times must be measured over years or decades, as opposed the daily or weekly response time of chemical features such as pH.

When considering soil microarthropod communities, our study indicates that the organisms in Val di Fassa were strongly affected by soil coverage conditions and, to a lesser extent, by pH. Similarly, microarthropod communities in Cansiglio were influenced by the interaction between soil condition and vegetation type, whether this was solely coniferous or mixed deciduous-coniferous. On the other hand, neither the type of humus system nor SOM was found to significantly affect microarthropod communities—a result which can be attributed to ongoing topsoil evolution after the storm, together with the lack of stability in the humus systems within windthrow areas. The classification of humus systems in these disturbed environments has proven to be a significant challenge. The difficulties in classification are compounded by several factors, including changes in climatic conditions, animal migration and the mixing of diagnostic horizons. The perception of horizon boundaries changes; for example, OH layers are found within the A horizon, or clusters of A horizon material are found within the OH horizon. This results in a new spatial arrangement of diagnostic horizons, which, instead of being superimposed as in an undisturbed system, form a vertical and/or horizontal mosaic. This complicates the classification of the disturbed humipedon, whose horizons no longer fit within the definitions of typical humus systems. Many of the humus systems we identified were disturbed, with a possibility of error. Another issue is the minimum thickness of a diagnostic horizon, which must be ≥ 3 mm for classification [40]. This "minimum detection level" was established to ensure visibility to the naked eye and to represent a threshold that was likely to impact ecosystem function. In the present case, observations of OH traces (thickness < 3 mm) above an A horizon were excluded from the classification, resulting in a Mull designation. Nevertheless, the presence of OH traces may signify a transition toward an Amphi or a Moder in terms of function. This may have introduced a bias in the comparison of humus systems with regard to arthropod presence, as these organisms could have been present in the OH clusters that we failed to observe. Consequently, we classified the humipedon as a Mull instead of another system with arthropods. We therefore propose that humus systems should always be considered in a dynamic context. Horizon clusters can contain numerous microarthropods, a factor with significant functional implications that allows humus systems to evolve from one to another with relative ease. Disturbed diagnostic horizons can lead to errors in the classification of humus systems. Soon, soil biodiversity studies will likely include the systematic extraction of DNA or RNA from each diagnostic horizon of the soil profile to identify the species and quantity of animals involved in humipedon formation. This approach will help to better characterize the active presence of biological agents within humus systems.

In the undisturbed sites of Val di Fassa, no significant differences were detected in the number of microarthropod groups or in the total abundances between intact forest sites and meadows, a result which contrasts with that reported by Menta et al. [25] who, within the same sampling areas, found lower abundances and fewer microarthropod groups in meadows compared with intact forest. In the windthrow sites of Val di Fassa, the number of microarthropod groups remained stable in soils under herbaceous vegetation cover when compared with intact forest but declined in soils under decaying wood, with bare soils exhibiting the lowest values recorded. In this last type of soil, only Acarina, Collembola, Diplopoda, Chilopoda and Symphyla were present, all with low abundances. This result is in line with Wehner [41], who found almost no microarthropods in post-disturbance bare soil. Interestingly, Menta et al. [25] reported that Diplopoda and Symphyla abundances did not differ significantly between intact forest and windthrow areas, suggesting a high adaptability of these taxa, probably due to their high mobility: horizontal for epi- and hemi-edaphic Diplopoda and both horizontal and vertical for Symphyla, a class that is known to perform vertical migration and express the highest abundances below the topsoil [42,43].

Symphyla is one of the neglected classes in the literature, with the little information available often being contradictory regarding its ecology, species distribution and response to natural disturbances. In our study sites, we observed that Symphyla abundance was affected by soil coverage conditions in windthrow areas, decreasing under decaying wood and increasing under herbaceous cover, with the highest values found in meadows. In a similar way, Symphyla in Cansiglio seemed to be favored by habitat changes, with numbers increasing in coniferous stands within windthrow areas. This result contrasts with some studies that have identified woodlands as the preferred habitat for Symphyla [44,45] and others that have reported a decrease in their abundance following forest disturbances [46,47]. However, our findings are in line with studies showing that several Symphylan species successfully colonize meadows and pastures [48] and are also present in forests regenerating after severe fires [49]. In addition, our results are consistent with a study that revealed greater Symphyla abundance in conifer forest clearings and regeneration stands compared with mature forest stands, in all likelihood a result of increased pH [50]; a pH increase was also observed in our study.

Total microarthropod abundance in windthrow areas exhibited a trend similar to that of the total number of groups across soil coverage conditions, albeit with variations among microarthropod groups and vegetation cover. In soils under decaying wood, Collembola exhibited a similar abundance to that occurring in intact forest sites, whereas the abundance of all the other groups declined. The high Collembola abundance in windthrow areas is consistent with a study by Čucha [17], which found that the abundance of this particular group initially decreased but then recovered to almost pre-storm levels after a three-year period. In contrast, Oribatid mite abundance was lower in meadows compared with intact forest sites, with the mite abundance decreasing in all windthrow areas, particularly in soils under decaying wood and with bare soils exhibiting the largest reduction. This is in line with Kreibich [51], who observed a decline in Oribatid mite abundance immediately after a storm and a subsequent slow increase after a four-year period. Overall, these results suggest that Collembola communities might recover faster than those of Oribatid mites following a wind disturbance. In Cansiglio, the decrease in Oribatid mite abundance in windthrow areas was more evident in mixed forests than in coniferous ones. This was probably due to the fact that Oribatid mites, most of which are fungal feeders [52–54], suffered from the loss of fungi-rich deciduous litter characterizing the damaged mixed forests.

Other groups of microarthropods revealed a contrasting response to wind disturbance in coniferous and mixed forest, similar to what was observed for Oribatid mites (a decrease in the number of non-Oribatid mites in windthrow areas with deciduous vegetation whereas their numbers doubled in coniferous vegetation sites); Protura abundance (50 times higher in intact mixed deciduous forests than in coniferous forests) was not affected in windthrow areas with coniferous vegetation but increased in windthrow-affected areas with mixed deciduous vegetation. In the case of Protura, considering that in Cansiglio, the highest abundance was found in soils under decaying wood, it could be hypothesized that this group was probably stimulated by the increased soil fungi growth on fallen wood in the damaged forests [55]. This is also in line with Sterzyńska et al. [26], who claimed that soil biogeochemistry and resource availability have a greater impact on the Protura group than forest disturbance.

Overall, all the microarthropod parameters analyzed in this study showed a declining trend in windthrow-affected areas in Cansiglio. Nevertheless, the variability in response among the different taxa among vegetation types illustrates the need for long-term studies to fully understand the ecological impacts of such disturbances in mixed coniferous forests. In fact, very few studies exist regarding soil communities in windthrow areas with deciduous vegetation in Europe, which is probably due to the fact that spruce is much more susceptible to windthrow than other broadleaf species.

Data from our study suggest that in windthrow-affected areas, the dissimilarities between microarthropod communities under different soil coverage conditions are increasing. Having said this, five years may be an insufficient period of time to observe more pronounced differences. Of all the conditions studied, bare soil is the most impacted. However, this particular environment will disappear over time following the rapid colonization of herbaceous vegetation, unless the erosion process continues to be present. This hypothesis is supported in a study by Duelli et al. [56], who found that different management practices in windthrow areas (e.g., clear-cutting or leaving dead trees in place) led to increased faunal species richness and dissimilarities between soil coverage conditions, particularly where epigeic insects are concerned, although these effects were only evident ten years after the time of the disturbance.

Finally, regarding the Shannon diversity index and the QBS-ar index, both remained stable across almost all the conditions but showed a significant decrease in bare soil. This suggests that the storm did not negatively affect either microarthropod diversity (at a high taxonomic level) or overall soil biological quality when the soil remained covered. It is the patchiness resulting from windthrow, therefore, that appears to be a main driver of microarthropod community diversification.

5. Conclusions

In this study, we characterized three distinct habitats depending on the soil coverage conditions in windthrow-affected areas (soils under herbaceous cover, soils under decaying wood and bare soils), each with its own soil properties and humus systems. Our findings indicate that in windthrow-affected soils, humus shifts from systems with medium-fast soil organic matter turnover to the Mull system, which is characterized by a faster soil organic matter turnover. An overall decrease in soil organic matter content across windthrow areas was, therefore, observed, with this shift being more pronounced in soils under herbaceous cover, where there was a thinner O horizon, similar to the conditions in permanent meadows. Under decaying wood, however, where a thicker O horizon layer was maintained, this shift was less pronounced. Bare soils represented the most extreme condition, albeit a transient one.

No discernible link was found between the arthropod community structure and the humic system, probably because the diagnostic horizons were mixed, and it was difficult reduce these to a typical diagnostic horizon, and the soil microarthropod communities are still evolving and not yet stabilized/stratified in the profile. However, the microarthropod communities exhibited significant dissimilarity in different soil coverage conditions. Our results, therefore, highlight the fact that varying soil conditions enhance community dissimilarity, thus supporting the thesis that windstorms do not have an inherently destructive effect on forest ecosystems but rather present an opportunity for the enhancement of microarthropod diversity. This result underlines the importance of maintaining heterogeneous soil environments in post-disturbance management practices to support diverse biological communities.

In particular, our study underscores the ecological necessity of not clearing all windthrow-affected soils—leaving decaying wood in place not only enhances biodiversity but also serves as a crucial source of soil organic matter, facilitating soil health and resilience.

Finally, our study emphasizes once more that the evolution of these systems is quite slow. With catastrophic storms potentially becoming more frequent in the future due to climate change, it is uncertain whether forest ecosystems will have sufficient time to recover. Addressing this concern will require more long-term studies to monitor recovery processes and to better understand the level of resilience these ecosystems can summon in a changing climate scenario.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land13091458/s1, Figure S1: FAMD graph representing the relations between all the quantitative and qualitative variables from the two sampling areas, Table S1: Generalized linear model (GLM) results for the Val di Fassa and Cansiglio areas. Spreadsheet S1: Complete microarthropod abundance data.

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