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Windthrow Disturbance Effects on Alpine Forest Humipedon: Linking Organic Matter Dynamics, Humus evolution, Microarthropod communities and Ecosystem Management

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Dottoranda

Dott.ssa Visentin Francesca

Supervisore

Prof.ssa Menta Cristina

Co-Supervisore

Prof. Zanella Augusto

Coordinatore

Prof. Cavalieri Duccio

ABSTRACT

Natural disturbances are an integral part of forest ecosystems and play a key role in forest regeneration. The most important natural disturbance in Europe and the one that causes the most damage to trees is wind. Climate change is increasing the frequency and intensity of these phenomena and it is becoming increasingly important to understand the impact of these events on forest dynamics to set management strategies that minimize damage and increase the resilience of European forests. The impacts of windthrow on soils can be locally very severe and include a loss of canopy and exposure of soil surface layers to solar radiation, an accumulation of plant material on the soil, a mixing of soil horizons and organic matter due to tree uprooting and a loss of organic carbon, resulting in a great heterogeneity of microhabitats in the affected areas. These changes are expected to heavily influence soil microarthropod communities, humus formation and carbon sequestration dynamics. Despite their importance for forest recovery, these post-disturbance dynamics are seriously understudied.

In this context, the PhD research had the following objectives: (i) to characterize the different microhabitats resulting from windthrow damage; (ii) to study the evolution of humus profiles within these microhabitats and assess whether they correlate with soil coverage conditions; (iii) to characterize the microarthropod communities within the microhabitats and determine whether a discernible link exists between microarthropod communities, humus systems, or soil coverage conditions; (iv) to determine whether specific microarthropod taxa or humus forms may serve as indicators of habitat change; and (v) to provide recommendations for the sustainable management of windthrow-affected areas. To achieve these objectives, the research activity was divided into two phases, a first, broader one focusing on humus dynamics in both undisturbed and disturbed environments, and a second one focusing on the study of the functional relationships existing between microarthropod communities, humus forms and organic matter dynamics in areas affected by windthrow.

Research showed that: (i) Ground cover drives microhabitat diversification. In the windthrow areas, soils with vegetation cover and bare soils had thinner organic horizons, topsoil pH and respiration increased and organic matter decreased compared to intact forest soils, making them resemble permanent meadow conditions. This occurred to a much lesser extent in the soils under dead wood, protected from direct irradiation; (ii) Windthrow-affected areas showed a shift from the Amphi humus form, typical of forests, to the Mull form, characteristic of meadows and of more biologically active forest soils; (iii) Microarthropod communities responded differently across microhabitats. Significant structural differences were observed between communities under different soil covers, though community diversity and soil biological quality remained stable (except for a notable decline in bare soil) indicating a certain degree of resilience of the humipedon; (iv) Humus has potential as an ecological indicator, though further validation is required; (v) Maintaining soil heterogeneity is crucial for forest recovery. Windthrow disturbances create diverse soil conditions that may enhance microarthropod diversity. However, humipedon development is a slow process, raising concerns about whether forest ecosystems can recover adequately if disturbance frequency continues to rise.

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PRELIMINARY REMARKS

The rationale for this research project is based on the recognition of significant gaps in our understanding of the dynamics of humus and its relationship with edaphic fauna and forest dynamics. The research community has historically demonstrated only marginal interest in soil as an ecosystem, rather than merely as a substrate. However, in recent decades, the critical role of soil as a biodiversity reservoir and primary source of ecosystem services has come to the fore, and interest in this area is rapidly increasing. There is a growing awareness of the pivotal role of soil in the stability of terrestrial ecosystems and of the multitude of functional relationships between soil biota, vegetation, mineral components and climate. Many of these relationships have been investigated, yet some remain poorly understood. Particularly regarding soil fauna, it is estimated that only 10% of the communities has been sampled, and the biology and function of numerous groups are virtually unknown (Coleman et al., 2018). In light of the accelerated pace of climate change, it is imperative to comprehend its impact on these relationships and the potential consequences on the capacity of soils to sustain essential ecosystem services for human survival.

The severe windstorm named “Vaia”, that struck northern Italy in 2018, resulting in extensive forest damage, presented a unique opportunity to investigate relationships between soil fauna and humus dynamics in the aftermath of an extreme weather event.

AIMS OF THE STUDY

The evidence indicates that climate change has a positive effect on the frequency and intensity of catastrophic storms in Europe, which in turn causes extensive damage to forests. At the same time, an increase in tree uprooting appears to decrease carbon storage in soils, acting as positive feedback on increasing CO_2 concentrations in the atmosphere. Humipedon is capable of sequestering organic carbon, and its formation strictly depends on the interaction between abiotic factors (as climate) and biotic compartment (among others, vegetation and edaphic fauna). However, there is a paucity of research examining edaphic animal communities and their functional and dynamic interactions with the evolution of humipedon in a disturbance context such as storm Vaia. This study is among the first to specifically examine the interactions between the evolution of humus systems and microarthropod communities following windthrow disturbance. The investigation of these interactions may provide innovative insights into the management strategies to be employed in areas affected by such events, within a framework of integrated environmental management aimed at reducing climate-altering emissions. This is particularly important in the alpine region, a hotspot of climate change. It therefore becomes important to understand these dynamics both for a macroscopic purpose, as a strategy to reduce global carbon emissions, and from a more local point of view, as forests provide essential ecosystem services to the people living in the area, the most important of which are: access to clean air and water, protection from landslides and avalanches, nutrition, health and recreation, carbon sequestration.

The project objectives are:

1) To characterize the various microhabitats resulting from windthrow damage in two Italian Alpine forests in terms of soil coverage and chemical soil parameters.
2) To study the evolution of humus profiles within these microhabitats and assess whether they correlate with soil coverage conditions.
3) To characterize the microarthropod communities within the same microhabitats and determine whether a discernible link exists between microarthropod communities, humus systems, or soil coverage conditions.
4) To determine whether specific microarthropod taxa or humus forms may serve as indicators of habitat change
5) To provide recommendations for the sustainable management of windthrow-affected areas with the goal of maintaining forest resilience.

In order to achieve the aforementioned objectives, the research activity was conducted in two phases over a three-year period. During the initial phase of the doctoral programme, the focus was set on humus. The classification was reviewed, the dynamics of humus in forest ecosystems were studied, and finally, based on this work, the evolution of humus after wind disturbance was investigated.

The second part of the research activity focused on the study of edaphic microarthropod communities in windthrow-damaged areas and their relationships with humus forms and organic matter dynamics.

The structure of the thesis reflects these two blocks of research and contains a section presenting the research work on humus and its dynamics, firstly in undisturbed and then in disturbed forest environments, and a second section presenting the work focused on the study of the dynamics of microarthropod communities.

1. INTRODUCTION

1.1 HOW CLIMATE CHANGE IS IMPACTING FORESTS ECOSYSTEMS

The world climate is changing. Human activity is unequivocally the cause of an increase of 1.1°C of global surface temperature since 1859-1900 period, according to the latest IPCC report ((IPCC, 2023). The same report states that "unless there are immediate, rapid and large-scale reductions in greenhouse gas emissions, limiting warming to close to 1.5°C or even 2°C will be beyond reach".
Global warming is not expressing in a uniform manner across all ecozones, in fact, there is a possibility that European mountainous regions may experience a relatively higher increase in temperature compared to the surrounding regions. A case in point is the Alps, where temperature rises have been observed to be twice the global average over the past century (Auer et al., 2007). Furthermore, the changes in precipitation amount and patterns in mountainous regions are subject to a considerable degree of uncertainty and these changes will be strongly influenced by the local geomorphological characteristics (Albrich et al., 2020).

Climate change has profound direct and indirect impacts on forest ecosystems. It can alter productivity and health of forests as well as the species distribution (Das, 2004; Delzon et al., 2013; Norby et al., 2007Garrett et al., 2006; Menéndez, 2007); it can alter the precipitation and moisture regimes and result in an augmentation of the drought-induced mortality (Allen et al., 2010); it can result in changes in the patterns of disturbance by forest pests (Allard & Moore, 2008); and it will increase the frequencies of extreme events, like drought, windthrow events and fires, while management choices such as promoting conifers and increasing standing timber volume can increase forest susceptibility to these disturbances (Lindner et al., 2010; Seidl, Fernandes, et al., 2011a). At this regard, Seidl et al. (2011a,b;) found that about half of the observed increase in disturbance impact in European forests over the period 1958-2002 (for fires, storm and bark beetles) could be attributed to climate change, while the other half was attributed to anthropogenic changes in the state of the forest.
Regarding European forests, the available data indicate a discernible and statistically significant upward trend in disturbance over time (Gregow et al., 2017; Senf & Seidl, 2021). This is evidenced by an average increase in the total volume of timber subjected to disturbance of approximately 845,000 m^3 per year between 1950 and 2019. Over the past 70 years, wind has been the primary cause of damage to European forests, accounting for 46% of the total timber volume disturbed, followed by fire and bark beetle infestations, representing 24% and 17% of the total, respectively (Patacca et al., 2023).

Natural disturbances such as wind, flood, drought, and fire have shaped ecosystems and organisms for millennia, with their influence on the structure and function of ecosystems being long recognized (Franklin et al., 2002; Thom & Seidl, 2016; Ulanova, 2000). Particularly, In European forests, windthrows, along with fire and burrowing, are classified

as pulse disturbances, are considered integral to forest ecosystem dynamics and soil fauna and trees have adapted to face the characteristic disturbance regimes of the ecosystems in which they evolved (Bengtsson, 2002). Indeed, indicators of biodiversity are seen to be positively affected by disturbances (Thom & Seidl, 2016). Windthrows are also acknowledged to play a key role in forest regeneration: they in fact leave biological legacies (standing dead trees, logs and stumps) and structural legacies (damaged and undamaged live standing trees) and create a microsite spatial eterogeneity that establish new cohorts of trees and enhance regeneration at different temporal scales (Franklin et al., 2002; Ulanova, 2000).
Despite their fundamental role in European forest ecosystems, with climate change accelerating, the extent of forest disturbance is expected to increase dramatically. For example, the volume of timber damaged annually in Europe is projected to rise by 229.4% during the period 2021–2030 compared to 1971–1980 (Seidl et al., 2014). Under these conditions, the recovery dynamics and overall resilience of soil animal communities may be significantly affected, potentially altering ecosystem processes in ways not yet fully understood.

In fact, while forests demonstrate considerable adaptive capacity in response to gradual climatic shifts, they are nevertheless particularly susceptible to anthropogenic climate change. This is due to the extended lifespan of trees, which precludes the possibility of rapid adaptation to fast environmental changes. (Lindner et al., 2010). Despite the inherent difficulties in studying resilience in forest ecosystems, two recent studies have demonstrated that forest resilience may be on the decline. Albrich et al. (2020) identified substantial shifts in forest composition and size structure in their study site in the European Alps in response to climate change. Forzieri et al.(2022) demonstrated that tropical, arid and temperate forests are experiencing a significant decline in resilience, which is likely associated with increased water limitations and climate variability. In light of this diminished resilience, it can be expected that the observed intensification of disturbance regimes (defined as an increase in the frequency and severity of disturbances) will have a detrimental impact on the services provided by forest ecosystems to society, including their potential to act as a carbon sink (Lindner et al., 2010; Seidl et al., 2014).

1.2 WINDTHROW DAMAGE ON EUROPEAN FOREST STANDS

Since 1950 more than 130 storms have been recorded causing notable damage to forests in Europe with on average two destructive storms each year (Gardiner, 2013).

The susceptibility of individual trees and tree stands to wind damage is controlled by the properties of the wind (wind speed, duration and gustiness), forest structure (e.g. fragmentation, even-aged/uneven-aged), tree/stand characteristics (e.g. species, height, diameter at breast height, crown and rooting characteristics and stand density), and site conditions (e.g. soil type and topography). Specifically, the probability of damage or uprooting increases with increased height of the stand and density, increases if the stands are monospecific and even-aged, and some species, like the conifers (particularly the spruce) are more vulnerable than broadleaved species. (Albrecht et al., 2012; Gardiner, 2013; Mitchell, 2013; Motta et al., 2018; Schindler et al., 2012; Schmidt et al., 2010).

Generally, tree and stand characteristics appear to have more impact on tree and stand vulnerability than site characteristics, but with wind speed exceeding 100 kmh^{-1} per tree (or 150 kmh^{-1} for the most resistant species), every stand can be impacted. (Gardiner, 2013; Virot et al., 2016). Under this limit, the vulnerability of the stand can be reduced with good forest management choices (Motta et al., 2018).

Wind disturbances, such as windthrow events, can have profound and lasting effects on forest soil properties, leading to significant but understudied structural changes in the topsoil. One of the most evident consequences is the deposition of dead trees and canopy materials, like branches and leaves onto the forest floor, contributing to an increase in deadwood supply (Lugo, 2000; Shiels & González, 2014). Wind-uprooted trees often create characteristic pit-and-mound reliefs, resulting from the upheaval of root systems, which can invert mineral soil and organic layers and redistribute soil horizons and soil organic matter (SOM) down to the bedrock (Clinton and Baker, 2000).

These events combined can induce local changes in soil chemistry and hydrology and can modify soil porosity and structure, while the exposure of topsoil layers to solar radiation following canopy loss elevates soil temperatures and stimulates microbial activity and therefore soil respiration. This can lead to increased CO_2 emissions, loss of soil organic carbon and a reduction in the soil organic matter C:N ratio. (Kramer et al., 2004; Lüscher, 2002; Mayer et al., 2017).

Changes at both micro- and macrohabitat level caused by such disturbances affect soil population structures and the balance of soil trophic chains (Čuchta et al., 2012; Lóšková et al., 2013), but the real impact on windthrow on soil biome is still unclear. Studies on soil microorganisms have reported varying results; however, findings suggest that these communities are not significantly affected by windthrow. Instead, they appear to be more influenced by the microclimatic conditions resulting from the presence or removal of dead wood. Moreover, windthrow does not seem to produce a significant impact on the functional diversity index of microorganisms in the studied soils (Gömöryová et al., 2011; Gömöryová et al., 2014; Gömöryová et al., 2017; Waring et al., 2024; Wasak et al., 2019). Since humus, which forms through the interaction of mineral components, climate, vegetation, and soil biodiversity, depends on the decomposition of plant residues by animals, bacteria, and fungi (J. F. Ponge, 2003; Zanella, Berg, et al., 2018), these shifts in the decomposer community and soil trophic chains influence the dynamics of humus formation, impacting ecosystem stability (Coyle et al., 2017).

Windthrows result therefore in an extremely heterogeneus environment, creating a patchy structure in disturbed forest ecosystems (Beatty & Stone, 1986; Bormann et al., 1995; Schaetzl et al., 1989; Ulanova, 2000).

1.3 THE CASE OF THE "VAIA" STORM

The latest large-scale wind disturbance event to affect Italy was the case of the storm "Vaia": Between the 28th and the 30th of October 2018, a severe windstorm hit the north-eastern sector of the Italian Alps. Warm sirocco winds, boosted by their passage over the warmer than usual Mediterranean Sea (1-2°C above the mean of October), met cold air descending from northern Europe resulting in exceptional rainfalls and hailstorm in different parts of Italy. The inflow of cold air fueled a strong depressional vortex in northern Italy, which led to the strengthening of the sirocco and libeccio winds that exceeded, in some close valleys, the speed of 200 kmh^{-1}, pushing the Beaufort classification of this perturbation between "violent storm" and "Hurricane". Several weather stations of some alpine municipalities of Veneto, Friuli-Venezia Giulia e Trentino-Alto Adige registered in three days record rainfalls for those areas, reaching for example 715mm of rain in Soffranco (BL) and 817mm in Malga Chiampuz (UD). (ARPAV, 2018; NIMBUS, 2018)
Vaia storm affected 494 municipalities, the most affected regions being Trentino-Alto Adige and Veneto, followed by Lombardy and Friuli-Venezia Giulia. An estimated area of 42,500ha of partially or completely damaged forest was calculated, for almost 8,500,000 m^3 of timber on the ground. Based on these estimates, the Vaia storm is the most destructive event ever recorded in Italian forests (Chirici et al., 2019; Motta et al., 2018; Zanella et al., 2020).

In order to achieve the project objectives, two areas among the most significantly impacted by this storm were selected for investigation: one in the Veneto region and one in the Trentino-Alto Adige region. Several research plots were established within each area, and the fieldwork were conducted five years after the disturbance.

2. HUMIPEDON CONCEPT AND ITS DYNAMICS IN WINDTHROW-DAMAGED FORESTS

With the intent of better understanding the functioning of soil as an ecosystem (Ponge, 2015), it has recently been proposed to subdivide the entire thickness of soil into three subunits, each with distinct functional characteristics: Humipedon, Copedon and Litopedon (Zanella, Ponge, et al., 2018). From the bottom to the top, the Litopedon comprises the rocky mineral horizons (R, C); the Copedon comprises the mineral horizons of recent formation (B, E); and the Humipedon consists in the organo-mineral and organic horizons, comprising the fresh litter (A, O). The humipedon, in particular, is the most superficial part of the soil, in contact with the atmosphere or a water body, in which dead organic matter accumulates and/or mixes with the mineral component. Humipedon is dominated by bioturbation processes driven by soil biota and undergoes monthly variations whereas the entire soil profile takes centuries, or even millennia to form and change under normal conditions.
Since soil biota not just inhabits the soil but actively modify its natural framework, creating an ecological dynamic system, the most effective way to understand soil functioning is by studying the multitude of interactions within the Humipedon between plants, animals, and microbes (Ponge, 2013).

Soil organic matter is degraded and mixed with mineral components by soil biota across various spatial scales, from the macro-scale of large soil-dwelling mammals to the micro-scale of soil microorganisms. Each component of this process is highly interconnected with the entire system and is influenced by the abiotic factors within the ecosystem. The result of these processes is the formation of organic, organo-mineral, and mineral soil layers, which are functionally distinct but interconnected, known as Humus horizons. Since terrestrial ecosystems vary widely in terms of climate, nutrient availability, vegetation types, and soil biota, such systems of interactions between biotic and abiotic components taking place in the humipedon will be characterized by different Humus horizons and are called “humus interaction systems” or in short “humus systems” (Zanella, Berg, et al., 2018).

Prior to undertaking a study of humus dynamics following a wind disturbance, it was imperative to have a robust understanding of humus classification and be able to accurately assess its dynamics within an undisturbed forest ecosystem. Once these fundamental research objectives had been met, it became possible to embark upon the investigation of the impact that a disturbance might have upon these dynamics.
This research phase yielded three scientific papers, two of which have been published in academic journals and one of which is currently under review.
This papers, each with a specific aim, are presented in the following paragraphs:

1) Zanella, A.; Ponge, J.-F.; Jabiol, B.; Van Delft, B.; De Waal, R.; Katzensteiner, K.; Kolb, E.; Bernier, N.; Mei, G.; Blouin, M.; Menta, C.; Visentin, F.; et al. A Standardized Morpho-Functional Classification of the Planet’s Humipedons. *Soil Syst.* **2022**, *6*, 59. https://doi.org/10.3390/ soilsystems6030059

Specific aim: To present a modified and updated classification of the Humipedon, developed with the goal of standardizing humus classification on a global scale, making it easier to understand and more practical for use not only by scientists by also for soil managers

2) Zampedri, R.; Bernier, N.; Zanella, A.; Giannini, R.; Menta, C.; Visentin, F.; Mairota, P.; Mei, G.; Zandegiacomo, G.; Carollo, S.; et al. Soil, Humipedon, Forest Life and Management. *Int. J. Plant Biol.* **2023**, *14*,571–592. https://doi.org/ 10.3390/ijpb14030045
   Specific aim: To clarify the dynamics of humus in forest ecosystems through data review, comparisons between French and Italian investigation and the elaboration of new original data. Understanding these dynamics is not only essential for comprehending forest ecosystem functioning, but also for developing forest management strategies that are truly sustainable in a climate change context
3) Visentin, F.; Zanella, A.; Remelli, S.; Menta, C. Evolution of Forest Humipedon Following a Severe Windstorm in the Italian Alps: A Focus on Organic Horizon Dynamics. *Forests* **2024**, *15*, 2176. https://doi.org/10.3390/f15122176
   Specific aim: To examine the evolution of organic horizons and humus forms after the passage of "Vaia" windstorm under varying soil cover conditions, providing a comprehensive characterization of new habitats formed in the forest following the disturbance and identifying the drivers of that evolution.

2.1 HUMUS CLASSIFICATION

The necessity for the classification of the topsoil, with a particular focus on organic layers, emerged towards the end of the nineteenth century. This was prompted by Müller's observations in Danish forests, which indicated that the rate and type of decomposition of soil organic matter, as well as their incorporation with the organo-mineral component, were dependent on the specific type of forest and the prevailing local climate. These initial observations resulted in the delineation of three distinct 'humus forms', designated as Muld, Mor and Mullartiger, which were determined by the specific climatic, geological and biological characteristics that gave rise to their formation. Subsequently, many authors have made contributions to the classification of humus forms, with a particular focus on the key role of the biological component within the soil.

These concepts form the foundation of the subsequent classifications that have developed over the following decades, resulting in the establishment of two classification systems: one French and one Canadian. However, both classification systems were subject to limitations. Firstly, neither system was comprehensive in its coverage of all forest types and climatic conditions worldwide. Secondly, the parameters taken into account for classification differed between the two systems, which consequently renders the classifications not comparable (Zanella et al., 2011).

With the aim of harmonizing the classification and making it applicable in an European context, an initial group of experts met in 2003 in Trento (Italy) and formed the European Humus Group. Since then, the group has expanded and worked on a standardization of humus diagnostic characters validated on a European level also by non-experts and laid the foundations for a global extension of the classification method and the publication of an extensive classification key in 2018 (Zanella et al., 2018).

The article, entitled “A Standardized Morpho-Functional Classification of the Planet's Humipedons”, was born out of the necessity to modify the classification key in accordance with the findings of recent studies and to render it more accessible and practical for non-expert users.

soil systems

Review

A Standardized Morpho-Functional Classification of the Planet's Humipedons

Augusto Zanella[1,*], Jean-François Ponge[2,*], Bernard Jabiol[3], Bas Van Delft[4], Rein De Waal[4], Klaus Katzensteiner[5], Eckart Kolb[6], Nicolas Bernier[2], Giacomo Mei[7], Manuel Blouin[8], Jérôme Juilleret[9], Noémie Pousse[10], Silvia Stanchi[11], Fernando Cesario[12], Renée-Claire Le Bayon[13], Dylan Tatti[14], Silvia Chersich[15], Luca Carollo[1], Michael Englisch[16], Anna Schrötter[17], Judith Schaufler[16], Eleonora Bonifacio[11], Ines Fritz[17], Adriano Sofo[18], Stéphane Bazot[19], Jean-Christophe Lata[20], Jean-Francois Iffly[9], Carlos E. Wetzel[9], Christophe Hissler[9], Ginevra Fabiani[9], Michael Aubert[21], Andrea Vacca[22], Gianluca Serra[23], Cristina Menta[24], Francesca Visentin[24], Nathalie Cools[25], Cristian Bolzonella[1], Lorenzo Frizzera[26], Roberto Zampedri[26], Mauro Tomasi[27], Paola Galvan[28], Przemyslaw Charzynski[29], Elina Zakharchenko[30], Seyed Mohammad Waez-Mousavi[31], Jean-Jacques Brun[32], Roberto Menardi[1], Fausto Fontanella[1], Nicola Zaminato[1], Silvio Carollo[1], Alessio Brandolese[1], Michele Bertelle[1], Gaétan Zanella[33], Thomas Bronner[34], Ulfert Graefe[35] and Herbert Hager[17]

[1] Department Territorio e Sistemi Agro-Forestali (TESAF), Università degli Studi di Padova, 35020 Legnaro, Italy; luca.carollo.2@studenti.unipd.it (L.C.); cristian.bolzonella@unipd.it (C.B.); roberto.menardi@unipd.it (R.M.); fausto.fontanella@alice.it (F.F.); nicola.zaminato95@gmail.com (N.Z.); silvio.carollo@studenti.unipd.it (S.C.); alessio.brandolese@studenti.unipd.it (A.B.); michele.bertelle@studenti.unipd.it (M.B.)
[2] Museum d'Histoire Naturelle de Paris, Ecologie et Gestion de la Biodiversité, 91800 Brunoy, France; nicolas.bernier@mnhn.fr
[3] AgroParisTech, 75231 Paris, France; b.jabiol@free.fr
[4] Department of Environmental Sciences, Wageningen University, 6708 Wageningen, The Netherlands; bas.vandelft@wur.nl (B.V.D.); reindewaal@ziggo.nl (R.D.W.)
[5] Institute of Forest Ecology, Universität für Bodenkultur Wien, 1190 Wien, Austria; klaus.katzensteiner@boku.ac.at
[6] Fachgebiet Waldernährung und Wasserhaushalt, Technische Universität München, 85354 Freising, Germany; eckart.kolb@tum.de
[7] Department of Agraria, Mediterranea University of Reggio Calabria, 89122 Reggio Calabria, Italy; giacomo.mei@unirc.it
[8] Agroécologie, Institut Agro, INRAE, University Bourgogne, University Bourgogne Franche-Comté, 21000 Dijon, France; manuel.blouin@agrosupdijon.fr
[9] Department Environmental Research and Innovation (ERIN), Luxembourg Institute of Science & Technology (LIST), 4362 Belvaux, Luxembourg; jerome.juilleret@list.lu (J.J.); jeanfrancois.iffly@list.lu (J.-F.I.); carlos.wetzel@list.lu (C.E.W.); christophe.hissler@list.lu (C.H.); ginevra.fabiani@list.lu (G.F.)
[10] Office National des Forêts, 73000 Chambéry, France; noemie.pousse@onf.fr
[11] Department di Scienze Agrarie, Forestali e Alimentari (DISAFA), Università degli Studi di Torino, Grugliasco, 10095 Torino, Italy; silvia.stanchi@unito.it (S.S.); eleonora.bonifacio@unito.it (E.B.)
[12] Department of Geography (PPGG), Institute of Mathematical and Natural Sciences (CCMN), Federal University of Rio de Janeiro (UFRJ), Rio de Janeiro 21941-853, Brazil; fernandovieiracesario@gmail.com
[13] Functional Ecology Laboratory, University of Neuchâtel, 2000 Neuchâtel, Switzerland; claire.lebayon@unine.ch
[14] Hochschule für Agrar-, Forst-, und Lebensmittelwissenschaften (HAFL), 3052 Zollikofen, Switzerland; dylan.tatti@bfh.ch
[15] The Historical-Environmental Heritage Association, Corso Alessandro Tassoni 20, 10143 Torino, Italy; silvia.chersich@gmail.com
[16] Department of Forest Ecology and Soil, Federal Forest Research and Training Centre, 1131 Wien, Austria; michael.englisch@bfw.gv.at (M.E.); judith.schaufler@bfw.gv.at (J.S.)
[17] Department of Forest Biodiversity and Nature Conservation, Universität für Bodenkultur, 1180 Wien, Austria; anna.schroetter@students.boku.ac.at (A.S.); ines.fritz@boku.ac.at (I.F.); herbert.hager@boku.ac.at (H.H.)
[18] Department of European and Mediterranean Cultures: Architecture, Environment, Cultural Heritage (DiCEM), Università degli Studi della Basilicata, 85100 Matera, Italy; adriano.sofo@unibas.it
[19] Laboratoire Écologie, Systématique et Évolution—IDEEV, Université Paris-Saclay, 91190 Orsay, France; stephane.bazot@universite-paris-saclay.fr

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[20] Department Community Diversity & Ecosystem Functioning (DCFE), Sorbonne Université, 75006 Paris, France; jean-christophe.lata@sorbonne-universite.fr
[21] ECODIV, INRAE, Normandie Université, UNIROUEN, 76821 Rouen, France; michael.aubert@univ-rouen.fr
[22] Department Scienze Chimiche e Geologiche, Università degli Studi di Cagliari, 09124 Cagliari, Italy; avacca@unica.it
[23] Direzione Generale Protezione Civile, Regione Autonoma della Sardegna, 09123 Cagliari, Italy; lserra@tiscali.it
[24] Department Chemistry, Life Sciences and Environmental Sustainability, University of Parma, 43121 Parma, Italy; cristina.menta@unipr.it (C.M.); francesca.visentin@unifi.it (F.V.)
[25] Environment and Climate Unit, Research Institute for Nature and Forest, 49500 Geraardsbergen, Belgium; nathalie.cools@inbo.be
[26] Department Sustainable Agro-Ecosystems and Bioresources, Research and Innovation Centre, Fondazione Edmund Mach, 38098 Trento, Italy; lorenzo.frizzera@fmach.it (L.F.); roberto.zampedri@fmach.it (R.Z.)
[27] Studio Associato Pianificazione Ambientale Naturalistica (PAN), Sede Operativa di Merano, 39012 Merano, Italy; mautomasi@gmail.com
[28] Public Educational Institution, Istituto Comprensivo Pergine 1, 38057 Pergine, Italy; paola.galvan.km@gmail.com
[29] Department of Soil Science and Landscape Management, Nicolaus Copernicus University, 87-100 Torun, Poland; pecha@umk.pl
[30] Department Agrotechnologies and Soil Science, Sumy National Agrarian University, 40031 Sumy, Ukraine; elionapolis@gmail.com
[31] Faculty of Forest Sciences, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan 82834, Iran; waezmousavi@gau.ac.ir
[32] IRSTEA-Centre de Grenoble, Domaine Universitaire, 38421 Saint Martin d'Hères, France; jean-jacques.brun@irstea.fr
[33] Private Freelance iOS Developer, 75005 Paris, France; gaetan.zanella@gmail.com
[34] Private Freelance Android Developer, 73000 Chambéry, France; thomas.bronner@gmail.com
[35] Institut für Angewandte Bodenbiologie GmbH (IFAB), 22337 Hamburg, Germany; ulfert.graefe@ifab-hamburg.de
* Correspondence: augusto.zanella@unipd.it (A.Z.); jean-francois.ponge@mnhn.fr (J.-F.P.); Tel.: +337-8361-5957 (A.Z.)

Abstract: It was time to take stock. We modified the humipedon classification key published in 2018 to make it easier and more practical. This morpho-functional taxonomy of the topsoil (humipedon) was only available in English; we also translated it into French and Italian. A standardized morpho-functional classification of humipedons (roughly the top 30–40 cm of soil: organic and organomineral surface horizons) would allow for a better understanding of the functioning of the soil ecosystem. This paper provides the founding principles of the classification of humipedon into humus systems and forms. With the recognition of a few diagnostic horizons, all humus systems can be determined. The humus forms that make up these humus systems are revealed by measuring the thicknesses of the diagnostic horizons. In the final part of the article, several figures represent the screenshots of a mobile phone or tablet application that allows for a fast recall of the diagnostic elements of the classification in the field. The article attempts to promote a standardized classification of humipedons for a global and shared management of soil at planet level.

Keywords: humipedon; humus system; humus form; humusica; carbon cycle; soil classification; global change; soil biodiversity

1. Introduction: A Humipedon Classification Is Needed

There are abiotic and biotic soils [1]. Abiotic soils are, for example, the rocky surfaces of bodies evolving outside the Earth's atmosphere, such as the moon, Mars, and comets or asteroids. These abiotic soils correspond to rocks transformed by the actions of physical and chemical forces, in the absence of living organisms. True terrestrial soils have new functional characteristics that are very different from those of abiotic soils. These new features are purely of biotic origin.

All terrestrial soils are biotic soils (i.e., endowed of variable biological activity) and correspond to a biotic matrix made of living and dead organic substances, mineral substances, and a periodical or continuous dynamic fluid that connects the different parts of this living soil. A biotic soil acts as an ecosystem [2,3] where plants, animals, and microorganisms interact and use the physical and chemical environment [4,5] for building a living structure. When environmental conditions become difficult for the living beings inhabiting the soil (extreme temperatures and absence of liquid water, presence of high-energy radiations) [6], terrestrial soils resemble abiotic soils. The depth of the soil depends on this aspect; at a certain depth, microorganisms change/disappear [7–10], and the soil becomes a more or less abiotic substrate. Notice that even in harsh environment, surface rocky substrates are generally rich in microorganisms, and that in geological periods many rocks are themselves biogenic (i.e., limestone, coal, oil shale . . .) [11].

In scientific publications with the objectives of safeguarding and managing the environment, the survival of the planet's biodiversity is now presented as linked to a living soil matrix that guarantees its dynamic recycling and influences the planet's climate [12–18]. Indeed, in the course of geological times, the humipedon has behaved like the planet's air, changing as a consequence of the development of the biodiversity (microbial diversity, fundamentally), while remaining closely and indelibly connected with the biosphere as a whole [19].

Soil classification is important for exchanging knowledge among scientists and understanding how soil works [2]. In this moment of crisis in the planet's biodiversity [20–24], the ability to classify the soil becomes essential because a large number of living beings are found in the "topsoil" (which from now on in the text will be referred to as "humipedon") [25–29]. The humipedon corresponds to the organic (OL, OF, OH, and H) and organomineral (A, AE) soil-surface horizons, roughly the top 30–40 cm of a biotic earthly soil [30,31]. Knowing how to link the quantity and quality of organic matter (OM) in the soil [15,32–35] to the type of humipedon, enables a sustainable use of the soil for agricultural and forest purposes, and can contribute to climate-change mitigation [36–42]. A morpho-functional classification of the humipedon is now available [43]; accessible by direct naked-eye observation, or with the help of a 10 × magnification lens, some morphological characters allow a first understanding of the soil functioning. In particular, the observation reveals the vertical structure in horizons of the soil, and the biological actors of such a spatial organization. For example, it is possible to know how long it takes in natural conditions for a specific litter type to be integrated into the mineral soil [44]; or to recognize the main animal groups associated with the biodegradation (mineralization and humification), or the shape and size of their excrements [45].

To put it briefly, this classification corresponds to a rough distribution of all humipedons into 20 "humus systems"; the most common of these can even be subdivided into 3–4 more detailed "humus forms". An application can display dichotomous-like keys, photographs, and information on these humus systems and forms in three languages (English, Italian, and French). We present below an update of this classification that is valid for European temperate and Mediterranean terrestrial environments, and which has recently also become valid for Brazilian equatorial forests [46]. It has been used successfully in Iran, in the Caspian Hyrcanian temperate forests and in southern semiarid forest ecosystems in Zagros Mountains [47,48]; in Russia, trying to connect humus systems to the biological quality of the soil [14]; and France, comparing sites with mine deposits [49]. Recently, we have been testing the classification in Japan, on volcanic soils (to be published). Studies are underway to adapt the classification to agricultural [50] and urban [51] soils as well.

2. A Soil Parted in Subunits and Horizons

Soil as a whole is simply too complicated to understand. We need to break it down into functional subunits. We divided the body of insects into the head, thorax, and abdomen; for the soil it is useful to have three functional constituents too: Humipedon, Copedon, and Lithopedon. These sections arise from the fact that the soil-formation processes act both from above (actions of living organisms as plant roots, animals, and microorganisms with consequent litter recycling and formation of new organic components = Humipedon), and from below (weathering of the rock, water dynamics, bank of mineral elements = Lithopedon), converging at the center of the soil profile (formation of new mineral components, new physical environment = Copedon). These subunits are composed of layers called "horizons", and the attentive observer can understand how these horizons interact in each subunit, for a complex and harmonious functioning of the soil as a whole (Figure 1).

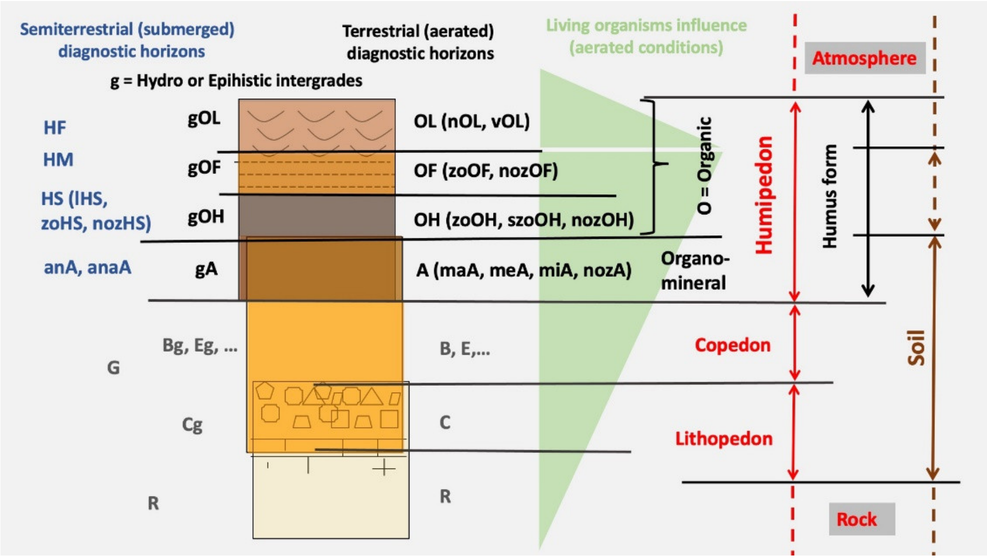


Figure 1. Soil subunits and horizons. From [43], modified (addition of Semiterrestrial diagnostic horizons). Humipedon horizons enlarged: Semiterrestrial Histic organic horizons [31] HF, HM, HS (lHS, zoHS, nozHS) and organomineral anA (Anmoor A horizon); Hydro and Epihistic intergrades horizons [52,53] gOL, gOF, gOH, gA; Terrestrial horizons "O" organic (OL, OF, OH; zo = zoogenic; noz = nonzoogenic; szo = slightly zoogenic) and "A" organomineral horizons (maA, meA, miA, nozA, respectively biomacro, biomeso, biomicrostructured, and nonzoogenic A horizons) [30]. Semiterrestrial humipedons may be very thick (peaty soils, until many m) or superficial (<1 m) and lying on hydromorphic Copedon and Lithopedon horizons; Terrestrial humipedons occupy approximately the first 30 cm of the profile, followed by the more mineral "E" and "B" Copedon horizons resting on "C" horizons and the weathered, altered "R" layer of the Lithopedon. Although organisms are present throughout the soil profile, they are more numerous in the Humipedon, for reasons related to the availability of nutrients and organic matter as a food resource. Reprinted/adapted with permission from Ref. [43]. 2019, *Soil Sci. Soc. Am. J.*

3. The Environment in Which the Targeted Humipedon Is Found

Soil organisms and biota activities evolve with the environment and generate horizons and subunits in tune with it. Once the vertical structure of the soil is unveiled and the humipedon is circumscribed, it is necessary to establish in which main "ecological frame" the observed topsoil is located. On a large scale, five sets of humipedons can be identified:

1. Terrestrial: humipedons that never submerged for more than a few days per year; peaty and water-filled horizons absent. These humipedons belong to Mull or non-Mull systems (Moder, Mor, Amphi, and Tangel);
2. Histic Semiterrestrial: submerged humipedons characterized by peaty horizons; presence of a water table (perched or not). These humipedons belong to Fibrimoor, Mesimoor, Amphimoor, Saprimoor, and Anmoor systems;
3. Aqueous Semiterrestrial: humipedons by the sea in tidal area, or submerged;
4. Para systems: humipedons connected to the other three groups (Para = next to) in a dynamic way; they either precede the others in time or develop with them (overlapped, juxtaposed). These are Archaeo (extremophile microorganisms), Anaero (submerged

organotrophic microorganisms), Crusto (cyanobacteria, lichens, algae, fungi), Rhizo (roots, rhizoids), Bryo (mosses), and Ligno (decaying wood agents) systems.

5. Anthropic systems: Agro (natural humipedons anthropogenically transformed for agricultural purposes) and Techno (manmade imitation of natural humipedons, e.g., compost, or without a specific purpose (waste dumps, etc.)).

Intergrades between Terrestrial and Semiterrestrial humipedons can also be identified using the Hydro prefix if hydromorphic features are present in a Terrestrial humipedons, or the Epihistic prefix when some Terrestrial horizons take place in Histic humipedons. The classification also enables us to recognize vertical and horizontal transitions, or mosaics between the above cited sets of humipedons (Figure 2).

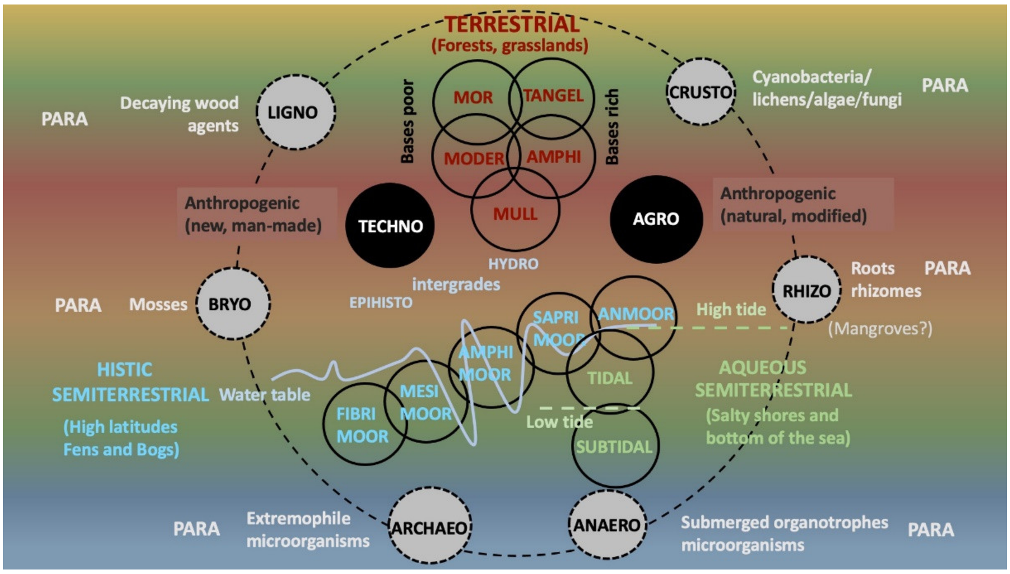


Figure 2. Slightly modified diagram (modified from [2]) showing all humus systems described in dedicated articles [44,52–56]. Terrestrial systems are placed at the top of a circle next to the Forests Grasslands title. They are divided vertically into non-Mull (Mor, Tangel, Moder Amphi) and Mull, and horizontally left to right into Bases poor (Mor and Moder) and Bases rich (Tangel and Amphi), with a nearly neutral Mull in between. Next to these, there are two anthropic systems, Techno (new systems manufactured by man) and Agro (natural systems modified by man for agricultural purposes) in black. Immediately below in blue are the partially submerged systems (Fens and Bogs, Histic systems), with a gray line indicating the oscillation of the water table (sometimes perched). From left to right of the figure, the systems pass from the permanently submerged Fibrimoor, to the Mesimoor, Amphimoor, Saprimoor, to arrive to the less-submerged (6 months per year, influenced by a slow oscillating water table) Anmoor. In the center of the circle, between the Terrestrial and Histic systems, there are the Hydro transitions closest to the Terrestrials', and Epihisto more similar to the Histics'. The systems dependent on daily tidal cycles, called Aqueous, and divided into Tidal (submerged at high tide) and Subtidal (submerged even at low tide), are shown in green-blue at the bottom left. In gray along the dashed circle are the Para systems, which correspond to particular stages of the evolution of the soil. Initial and progressive stages are with the nonsubmerged systems Crusto, Bryo, Rhizo, and Ligno, or submerged such as Archaeo and Anaero. One has likely already seen very common Bryo systems even on walls or roofs of houses; they are classified as Edifisoils by Markiewicz et al. [57]. These Para systems can exist alone or in combination with other systems. Reprinted/adapted with permission from Ref. [2]. 2018, *App. Soil Ecol.*

It is not possible to summarize the classification and complexity of humipedons in a few lines. For a precise general picture on the classification, we recommend reading the article "Essential bases—Quick look at the classification" [54]. More detailed information is published in articles 1 to 15 of two Special Issues [58,59]. Applications of classification and insights can be read in articles collected in a third Special Issue [60]. Below we present only the classification key of the Terrestrial and Semiterrestrial (Histic or Aqueous) systems, which are the most commonly considered in management or nature-protection plans. Their recognition key underwent a slight modification in 2020, abandoning the pH as a discriminating character. The role of parental material in the formation of the A horizon was preferred to pH, accompanied by characters related to tsoil structure and pedofauna.

4. Systems and Forms of the Main Terrestrial and Semiterrestrial Humipedons and Recent Advances in Humus Classification

There is a useful way to classify *Terrestrial humipedons*: packing them in five humus systems divided into 3–4 humus forms. Each system corresponds to a mode of operation. The Mull system is made of large worms' droppings, generally developing in temperate climate environments and on nonacidic rock (prevalent bacterial decomposition that incorporates all litter into the soil in a few months, in and out of the intestines of earthworms); the Moder is instead built by arthropods and enchytraeids in colder and more acidic environments; the Mor is mostly found in extremely cold and humid environments, and is poor in fauna (animals are very rare, prevalent fungal decomposition that generally takes a few years to integrate the litter into the soil); the Amphi, which arises in contrasting environments (alternately wet or dry, open or closed canopy, old or young sylvogenetic phases, etc.) is made up as a sandwich, composed of two separate layers: an A horizon formed by earthworms, on which lies a organic layer deriving from the activity of arthropods and enchytraeids; finally, the Tangel is typical of limestone mountain environments and resembles a Moder, with an increase in pH with depth, possibly with an A horizon in contact with a calcareous rock, the whole being very organic and exaggeratedly thick (Figure 3).

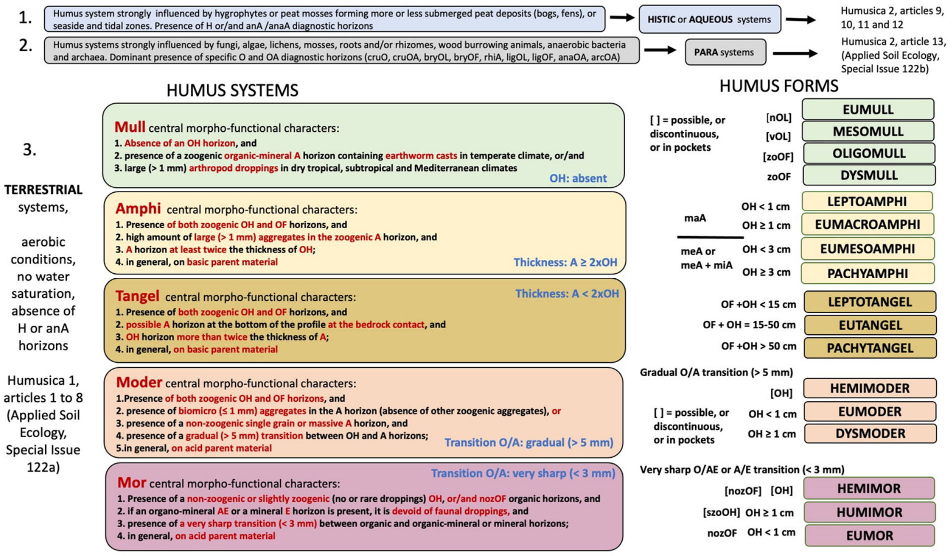


Figure 3. Main terrestrial humus systems (**left**) subdivided into humus forms (**right**). Modified from [44]. The first two sections at the top of the figure contain references to the diagnostic horizons that separate the Earth systems from the Histic, Aqueous, or Para systems. The characters to be considered for a quick classification of terrestrial humipedons are highlighted in red. A first quick and rough subdivision into the 5 systems could be the following: Mull: no OH horizon—it is a system determined by earthworms or large arthropods that completely consume all the litter; Amphi and Tangel: with OH horizon and generally on basic parent material (calcareous or high base saturation of topsoil horizons); Moder and Mor: with OH horizon and generally on acidic parent material (acidified topsoil horizons) or siliceous bedrock with low ANC (acid-neutralizing capacity); Amphi: with the thickness of the A horizon at least twice that of the OH horizon (it is a system determined by earthworms but in periodically arid environments); if the A horizon is less than twice the thickness of the OH we are in a Tangel (a system determined by arthropods in a calcareous and cold environment); Moder: with a gradual transition between the OH horizon and the A horizon (system dependent on

arthropods that are also able to colonize the mineral part of the soil); if the OH/A transition is well-defined, we are in a Mor (system with distinct separation of the organic and mineral part of the soil profile, generally determined by mainly fungal decomposition, in a cold and acidic environment). Reprinted/adapted with permission from Ref. [44]. 2018, *App. Soil Ecol.*

The organization of the key requires the classifier to first find the humus system to which the humipedon belongs. In the left large squares of Figure 3, the text highlighted in red defines each humus system in a simple and practical way:

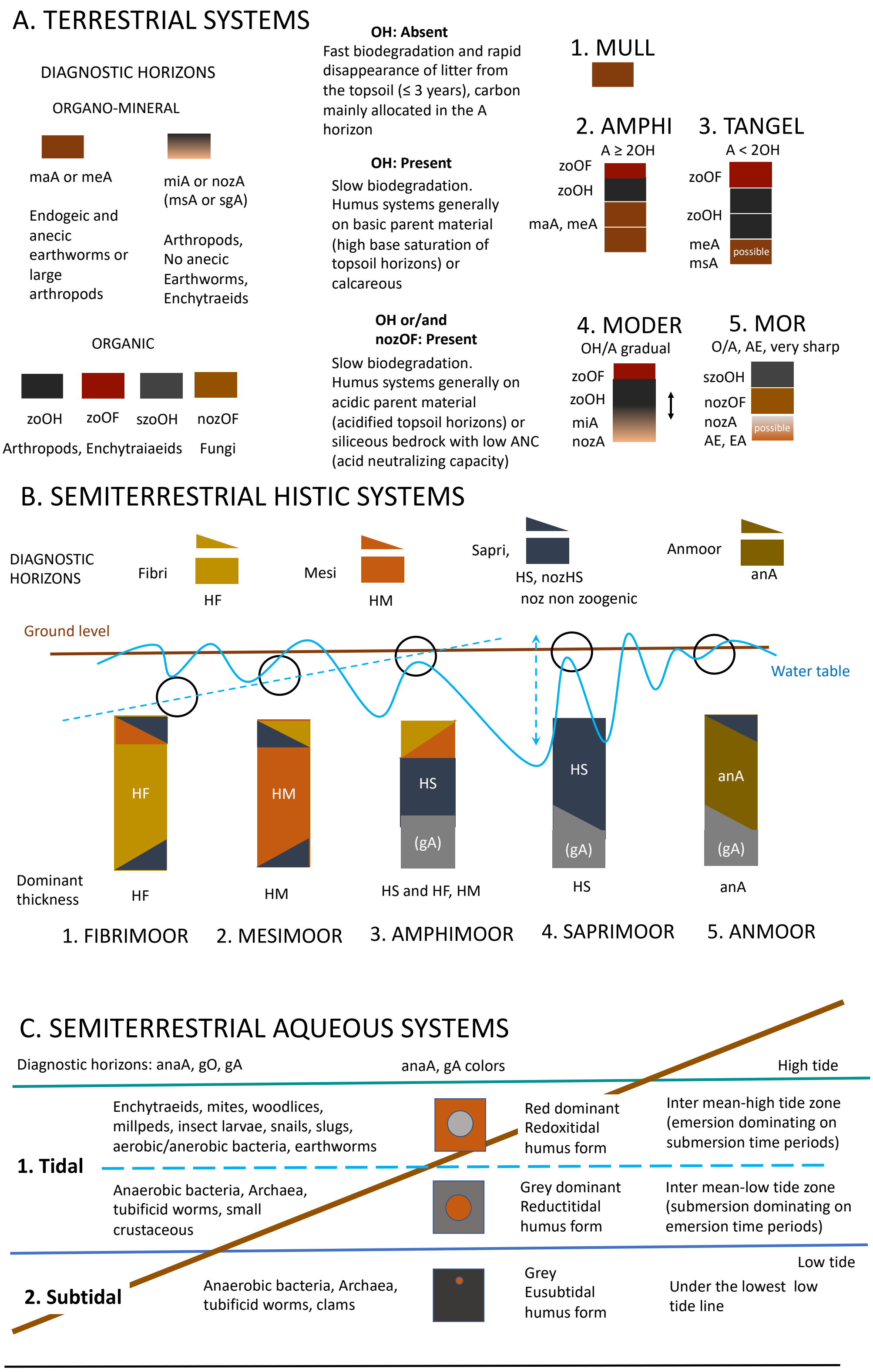
(a) Mull system (top square, absence of OH horizon = Mull system); or
(b) Non-Mull systems (with OH horizon = all the other systems):
    (b1) Non-Mull systems 1, on basic parent material (calcareous or high base saturation of topsoil horizons) divided according to the thickness of the OH and A horizons: if A $\geq 2 \times$ OH, Amphi, if A $< 2 \times$ OH, Tangel; or
    (b2) Non-Mull systems 2, on acidic parent material (acidified topsoil horizons) or siliceous bedrock with low acid-neutralizing capacity (ANC), divided according to the type of transition between the organic (O horizons) and organic-mineral (A) or mineral layers of the profile. If the transition is gradual, which means that migrant animals may form an organic-mineral A horizon, then it is a Moder. With a clear and sharp transition instead, which means that the soil fauna does not incorporate organic matter in the mineral matrix, it is a Mor.

During field investigations, this subdivision is very practical and is also shown in Figure 4A. This version of the key does not include pH as a diagnostic character compared to the taxonomic key presented in Special issue 122a in 2018 [44]. The pH helped to distinguish Moder from Amphi and Mull systems in Europe, but this parameter did not work in a tropical environment, where Mull and Amphi can have A horizons as acidic as in Moder conditions. Therefore, a universal key was adapted based on other characteristics, such as the structure and size of the aggregates, the thickness, and the transition between diagnostic horizons, which fit a more extensive set of ecosystems.

Two more words about the Amphi system, which does not seem to be known in other topsoil-classification references (https://forestfloor.soilweb.ca (accessed on 27 June 2022)) [61,62]: Usually the activity of the anecic worms results in the disappearance of the zoOF and zoOH horizons, and this generates a Mull. If these horizons persist on an A horizon built by earthworms, we obtain an Amphi. The situation of instability of organic zoOF and zoOH horizons is revealed by the presence of dejections and galleries of anecic worms. The Amphi system may be the result of a stable cohabitation of epigeic and endogeic earthworms, or of transient and dynamic anecic activity. This occurs in a situation of dry/wet or hot/cold alternation and along the sylvogenetic cycle [63]. For details on the classification and in-depth information, consult the Supplementary Materials 1.

Histic semiterrestrial humipedons have also been classified in a simple way (Figure 4B). The morpho-functional classification is based on the presence of a dominant horizon, or in one case on the equal value of two horizons, within the humipedon. In these moist environments, the humipedon can be very deep (>>1 m). For classification purposes, it was decided to limit the survey to the first 40 centimeters of humipedon [64]. The choice for a reference of a surface section of 40 cm comes from the ecological viewpoint that plant roots rarely go deeper into these asphyxiated environments, and from the practical and economic viewpoint that the agronomic use of these soils generally stops at this depth. Thus, five humus systems have been described, each divided into 3–4 humus forms, reaching a total of 13. The central and diagnostic features of each system are listed below:

Anmoor: within the control section (40 cm below the surface), presence of a dominant anA organomineral horizon; Zoogenic HS possible but never thicker than anA; humus forms of wet base-rich soils or soils enriched by base-rich groundwater around springs and in nondynamic parts of brook or river valley systems (parts of floodplains, lacking dynamic floods or inundations with fast currents);



Crusto, Mull and Moder as prefixes are often necessary to precise Redoxitidal humipedons

- Crusto: presence of aqueous litter laying on rock or mineral horizons without other humus horizons (example: Crusto Redoxitital);
- Mull: presence of anecic or endogeic earthworms; example Mull Redoxitidal
- Moder: presence of arthropods or epigeic earthworms, that can be associated to the origin of the gA horizon; example Moder redoxitidal

Figure 4. Schematizing the classification of Terrestrial (**A**), and Semiterrestrial Histic (**B**) or Aqueous (**C**) humus systems. Five morpho-functional systems are proposed for Terrestrial and Histic Semiterrestrial, and two of them for Aqueous Semiterrestrial.

Saprimoor: within the control section (40 cm below the surface), zoHS dominant (nozHS possible but thinner than zoHS), HF or HM never present within the first 40 cm; humus forms of moist base-rich mineral soils or eutrophic organic soils in mostly drained brook valley systems or fens and floodplains;

Amphimoor: within the control section (40 cm below the surface), presence of both zoHS and HM or HF, zoHS dominant, nozHS absent; humus forms of moderately moist base-poor soils in brook valley systems, or partly base-rich soils in half-drained fens;

Mesimoor: within the control section (40 cm below the surface), HF possible but never dominant, HM or nozHS present and thicker than other horizons; organic-matter degradation more active/efficient than in Fibrimoor; humus forms of wet, moderately base-poor organic soils in brook valley systems, or base-enriched soils of drained, previously base-poor fens or bogs;

Fibrimoor: within the control section (40 cm below the surface), presence of a thick HF horizon, HM possible but never thicker than HF, degradation of organic matter slow or inhibited; wet, very base-poor soils in brook valley systems and bogs, rain-fed moors, bogs, isolated parts of fens and brook valleys, base-poor, rain-fed soils. For details on the classification and in-depth information, consult the Supplementary Materials 2 (articles 9, 10 and 11).

Aqueous semiterrestrial humipedons are still under investigation [65]. They are distinguished from the Histic semiterrestrials by the more direct dependence on the sea (salt water and above all regular periodic dynamics of the tide). The diagnostic horizons are organic gO and organo-mineral anaA (anaerobic A) and gA (g = with hydromorphic features). In this particular medium, humus systems that form below the highest tide level and systems that develop above this level show different diagnostic horizons (Figure 4C). For the modality of interaction with plants, the former are more similar to Histic semiterrestrial systems, while the latter are more similar to Terrestrial ones. For details on the classification and in-depth information, consult the Supplementary Materials 2 (article 12).

Terrestrial (A):

- one Mull system without OH horizon, which corresponds to a rapid disappearance of litter from the topsoil;
- four systems with OH (or with organic horizons not or little-attacked by pedofauna), which corresponds to a slow process of litter biodegradation:
    - two influenced by calcareous (or basic) parent material systems: (a) A horizon dominates in thickness (Amphi); (b) OH horizon dominates (Tangel);
    - two influenced by siliceous parent material systems: (a) presence of biological interchange between organic and mineral horizons (Moder); (b) no interchange, no or very few pedofauna (Mor).

Semiterrestrial Histic (B):

- three long-time submerged systems (Saprimoor, Mesimoor, and Fibrimoor), with progressive submerged duration and characteristic dominant horizons;
- one disrupted system, with horizons showing a varying dynamic of submersion in time and duration, without a dominance of functioning revealed by a specific horizon (Amphimoor);
- one rather organomineral Anmoor system, in areas with long periods of flood or dryness (6 months), earthworms arriving when the soil becomes aerated.

Semiterrestrial Aqueous (C):

- one Tidal system that develops between the high and low tide levels. This system contains two humus forms which differ in the length of the submersion period. The "kinship" of the Tidal system with the Terrestrial systems can be highlighted by using suitable prefixes;
- one always-submerged Subtidal system lying under the lowest tide level.

Tested in various environments, this new key appears to work quite well. Examples of application of the classification are presented in Supplementary Materials 3. For the precise distinction of Terrestrial (non-submerged land) from other humipedons (submerged, young soils, anthropic systems), we suggest the reader to refer to dedicated articles [31,56,66]. Here, we present a freely downloadable iOS and Android application that allows an investigator to bring information connected to Terrestrial and Semiterrestrial Histic humus systems into the field, and to obtain some clues about common Para systems.

5. TerrHum: Humusica in Your Phones and Tablets

The TerrHum name assembles the abbreviated words Terra (planet Earth in Italian) and Humipedon (organic and organomineral humus horizons). With this application, a user can classify the Terrestrial and Histic semiterrestrial humipedons of our planet. It also contains some information on the diagnostic horizons of Para systems, such as the Bryo, Rhizo and Ligno, and on horizons disrupted by wild mammals. The application is built on the indications on the diagnostic horizons reported and illustrated in articles 4, 5, 6, 9, 10, 11, and 13.

The App is freely available on the iOS (App Store) and Android (Google Play) platforms in English, French, and Italian. TerrHum makes use of many figures that are stored in a cloud and downloaded on cellphones the first time the users recall them. Once all figures (about 140) have been opened, devices do not need to be connected to run the application.

Instead of describing the App, we show some figures that illustrate how it works (Figures 5–7).

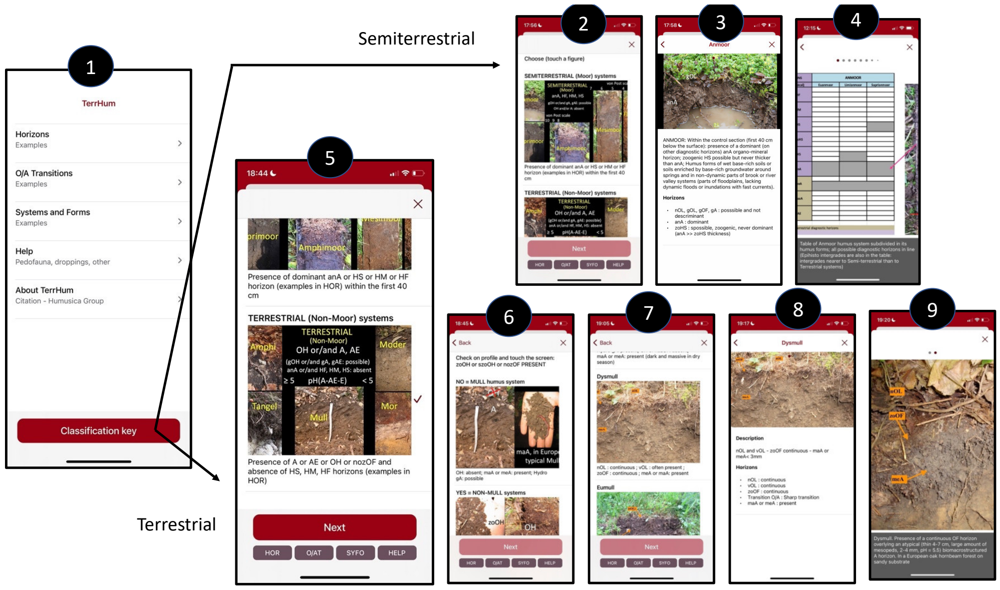
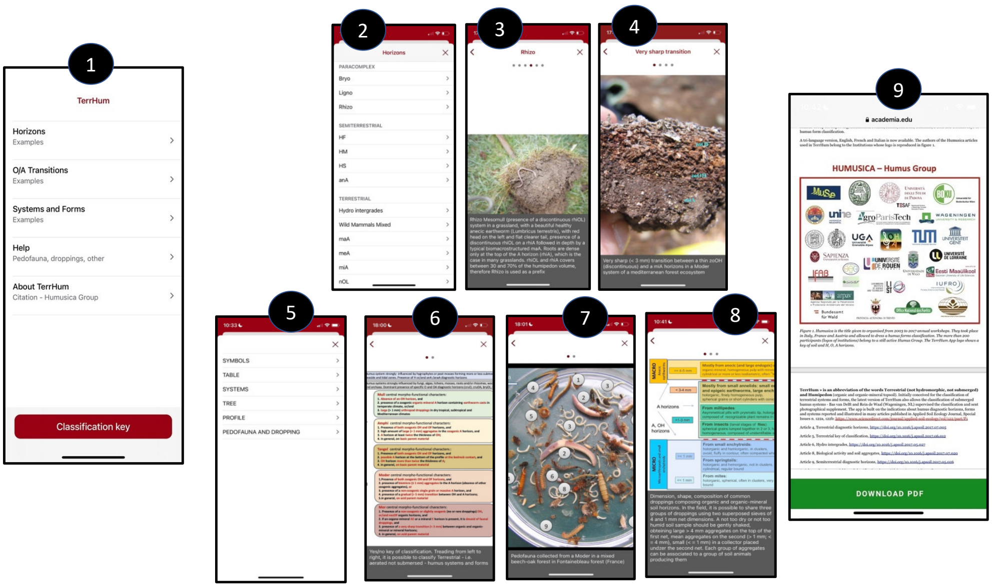


Figure 5. TerrHum is the result of a collective work and allows us to classify Terrestrial and Histic systems and forms. Indications are provided to also consider the Hydro transitions between Terrestrial and Histic, and also the complexifications of Terrestrial systems with Bryo, Ligno, and Rhizo systems. (1) Starting screen, iOS version (similar to the Android one). By clicking on the red button 'Classification key', the screen on the right opens; observing the profile to be classified, the user must choose between Semiterrestrial (2) and Terrestrial systems (5). To achieve this, they must search for the diagnostic horizons indicated on the screen. For example, to belong to the Semiterrestrial systems (2), a profile must show at least one of the following horizons: anA, HF, HM, HS; to belong to the Terrestrial systems (5), the profile must show OH, A, or AE horizons. If the user is a beginner, they can see photographic examples by tapping at the bottom of the screen (the four small brown rectangles at the bottom of screens 2, 5, 6, 7): HOR = diagnostic horizons, O/A T = O/A transitions; SYFO = systems and forms; HELP = tables, diagrams, other. These same commands correspond to the ones of the starting screen (1). Semiterrestrial example: By touching the screen at the "Semiterrestrial" level (2); ´Next´ appears in red, which allows one to move forward and scroll among examples of th-

ese humus systems; for example, by choosing ‘Anmoor’ between them, one can display some photographs of these system profiles (3). By touching the photo, one can zoom in by spreading one’s fingers on the screen. One can view more Anmoor examples, bringing the photo to the smallest size and sliding it to the left. Tapping the photo again brings up a legend. A table (4) with the details of the humus forms of this system can be viewed by pressing “systems and forms” on the screen (1), or the equivalent command “SYFO” at the bottom of other screens (2, 5, 6, 7). As with each image, the table can be enlarged by spreading the fingers on the screen. Terrestrial example: Terrestrial horizons are present on the real profile, the operator taps the Terrestrial figure (5); ´Next´ appears in red, which allows one to move forward (6). Now the operator has to choose between Mull or non-Mull systems. If there is an absence of OH horizon in the field profile, then the NO = MULL humus system figure should be selected, followed by ´Next´, to obtain examples of Mull forms (7). Then, it always works in the same way: by touching the screen at the level of the chosen figures, examples and legends appear that can be enlarged (8, 9). If in doubt, one can ask for information by clicking on the commands on the home screen (1) or at the bottom (small brow rectangles) of the other screens (2, 5, 6, 7).



Rhizo Mesomull (presence of a discontinuous rhiOL) system in a grassland, with a beautiful healthy anecic earthworm (Lumbricus terrestris), with red head on the left and flat clearer tail, presence of a discontinuous rhiOL on a rhiA followed in depth by a typical biomacrostructured maA. Roots are dense only at the top of the A horizon (rhiA), which is the case in many grasslands. rhiOL and rhiA covers between 30 and 70% of the humipedon volume, therefore Rhizo is used as a prefix

Very sharp (< 3 mm) transition between a thin zoOH (discontinuous) and a miA horizons in a Moder system of a mediterranean forest ecosystem

Yes/no key of classification. Treading from left to right, it is possible to classify Terrestrial - i.e. aerated not submersed - humus systems and forms

Pedofauna collected from a Moder in a mixed beech-oak forest in Fontainebleau forest (France)

Dimension, shape, composition of common droppings composing organic and organic-mineral soil horizons. In the field, it is possible to share three groups of droppings using two superposed sieves of 4 and 1 mm net dimensions. A not too dry or not too humid soil sample should be gently shaked, obteining large > 4 mm aggregates on the top of the first net, mean aggregates on the second (> 1 mm; < = 4 mm), small (< = 1 mm) in a collector placed undzer the second net. Each group of aggregates can be associated to a group of soil animals producing them

humus form classification.

A tri-language version, English, French and Italian is now available. The authors of the Humusica articles used in TerrHum belong to the Institutions whose logo is reproduced in figure 1.

Figure 1. Humusica is the title given to organised from 2003 to 2017 annual workshops. They took place in Italy, France and Austria and allowed to dress a humus forms classification. The more than 200 participants (logos of institutions) belong to a still active Humus Group. The TerrHum App logo shows a key of soil and H, O, A horizons.

TerrHum » is an abbreviation of the words Terrestrial (not hydromorphic, not submerged) and Humipedon (organic and organic-mineral topsoil). Initially conceived for the classification of terrestrial systems and forms, the latest version of TerrHum also allows the classification of submerged humus systems - Bas van Delft and Rein de Waal (Wageningen, NL) supervised the classification and sent photographical supplement. The app is built on the indications about humus diagnostic horizons, forms and systems reported and illustrated in many articles published in Applied Soil Ecology Journal, Special Issues n. 122a, 122b: https://www.sciencedirect.com/journal/applied-soil-ecology/vol/122/part/P1

Article 4, Terrestrial diagnostic horizons, https://doi.org/10.1016/j.apsoil.2017.07.005

Article 5, Terrestrial key of classification, https://doi.org/10.1016/j.apsoil.2017.06.012

Article 6, Hydro intergrades, https://doi.org/10.1016/j.apsoil.2017.05.027

Article 8, Biological activity and soil aggregates, https://doi.org/10.1016/j.apsoil.2017.07.020

Article 9, Semiterrestrial diagnostic horizons, https://doi.org/10.1016/j.apsoil.2017.05.026

Figure 6. Main screen commands (1): ‘horizons’, ‘O/A transitions’, ‘systems and forms’, ‘help’ and ‘about TerrHum’. ‘Horizon’ command opens screen (2). To list available horizons, just touch a horizon code on the screen and scroll for examples of this horizon. The user selected ´Rhizo´ (3); the dots above the figure indicate the number of possible views, and the 4th view corresponds to that of a Mesomull A horizon. A thin Rhizo system occupies the top. By spreading one’s fingers on the figure, one can zoom in. Touching the figure displays a legend. To go back, just touch the cross at the top right. ‘O/A Transition’ button allows one to see examples of gradual, sharp, and very sharp transitions between O and A horizons. The one enlarged on the screen (4) is a very sharp transition. ‘Systems and forms’ command is a shortcut for experts. It gives direct access to all the Semiterrestrial humus systems (to have the details of the Semiterrestrial humus forms, it is necessary to activate the ‘Help’ command and view the corresponding tables) and to all the Terrestrial humus forms, in alphabetical order. Just touch the name of a system or a form of humus to obtain examples of them. ‘Help’ button leads to a list of new commands (5): SYMBOLS = a list of symbols to be used in the field for the description of the diagnostic horizons (they were used in the field a few years ago; today we prefer to take a photo and write on it; however, sometimes batteries run out . . .); TABLE = humus systems classification tables and schemes; SYSTEMS = humus forms classification tables; TREE: dichotomous classification schemes (6); PROFILE = graphs on the soil structure in horizons; PEDOFAUNA AND DROPPING: photographs of animals (7) and droppings photographs and classification keys (8). ´About TerrHum´ leads to a web page with information on the Humus Group and on the articles from which the information presented with the app is taken. Researchers

from all the Institutes cited in the figure (9) were called to contribute. Once at a congress, someone objected that it is too complicated to classify humipedons. The answer was that the functioning of natural ecosystems is very interesting but complex.

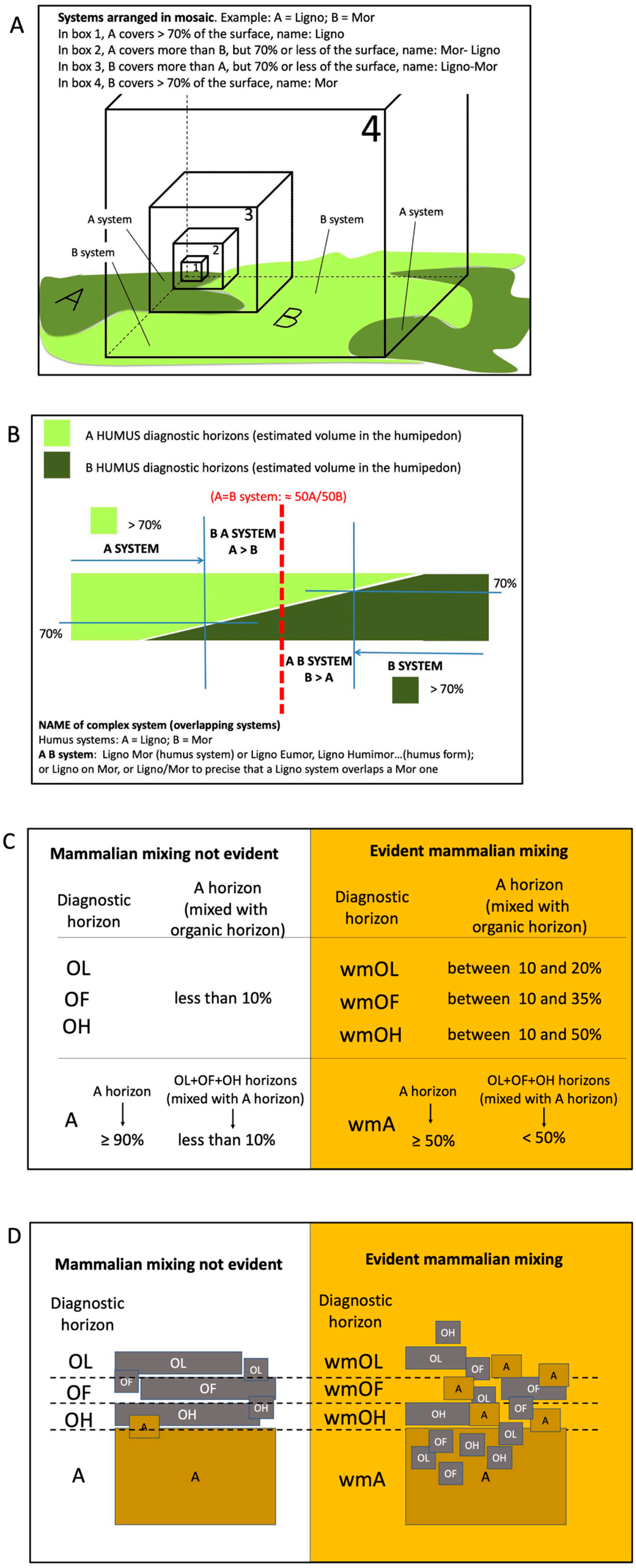


Figure 7. To simplify complexity: humus systems arranged in mosaic (**A**) or overlapping (**B**); diagnostic horizons broken down by wild mammals, definition (**C**) and schematic drawing (**D**). Generally, hum-

us systems juxtapose like pieces of a puzzle (**A**). To perceive this reality, it is necessary to investigate the environment at different scales and recognize the elementary humus systems. The interpretation of the landscape that follows depends on the observation scale. The figure shows an example of two humus systems, Ligno (dark green = a decaying stump) and Moder (light green = area without dead wood). In the smaller cube, there is only the Ligno system, in all the other larger cubes there are two systems. The name assigned to the system found in the studied environment depends on the dominance of one system over the other in the cube that contains that environment. Overlapping humus systems (**B**). This happens when studying series of soils along a large time gradient. In general, new systems arise under older systems. The genesis is recognized thanks to the presence of diagnostic horizons typical of different systems. The name that can be assigned to the humipedon analyzed depends on the thickness in the horizon profile typical of each system. TerrHum path: Main screen > Horizons > Ligno > Second (**A**) and third (**B**) pictures. Mammals, such as mice, moles, wolves, foxes, deer, wild boars, etc., can break down the horizons of a humipedon. These are based on the mixture of organic horizons with the organomineral A horizon (**C**,**D**). It is simply tolerated that in the event of obvious and localized turmoil caused by these animals, an organic horizon may contain more horizon A than usual, and that an A horizon may contain more organic material than usual. TerrHum path: Main screen > Horizons > Wild Mammals Mixed > First (**C**) and second (**D**) pictures.

6. Conclusions

TerrHum enables a standardized morpho-functional classification of the Humipedon (topsoil). The full citation reference for this application is as follows:

Humusica Group, 2022. TerrHum application 2022. From: Humusica Applied Soil Ecology Special issues vol. 122a and 122b, https://www.journals.elsevier.com/applied-soil-ecology/special-issues (accessed on 27 June 2022). Classification updated in December 2021. Android version (2022): Bronner T., Zanella A., Pousse N., TerrHum, Google Play, Education; original iOS application (2018, updated 2022): Zanella G., Zanella A., TerrHum, App Store, Education. Translated in French and Italian by: Tatti D., Ponge J.-F., Le Bayon R.-C., Chersich S., Stanchi S., Carollo L., Zanella A.

Advice for beginners:

(1) Humipedon classification cannot escape a part of subjectivity. Direct classification experience is an important component of diagnostic ability. The novice investigator should call on the knowledge of an expert, even if the key horizons are few: it is precisely necessary to know these fundamental landmarks with certainty. It only takes one outing to catch a glimpse and touch these horizons. In a terrestrial environment (= out of water), it is necessary to see the OH organic horizon and the maA and miA organo-mineral horizons; in a semiterrestrial environment (= more or less in water), the HF and HS organic horizons, and the anA and anaA organomineral horizons are crucial; to define the humipedons of the first stages of soil development, it is necessary to recognize at least the Crusto, Bryo, and Rhizo systems.

(2) In the field, humus systems and forms are distributed horizontally and vertically as in a mosaic (Figure 7A,B) [18]. It is therefore normal to be "lost" at the beginning. Before embarking on a localized and precise diagnosis, it is necessary to survey the ground, and determine the eventual main lines of the mosaic coverage. It is relatively easy to separate the Para systems from the others, for example, a Bryo systems on outcropping rocks. If in a phytocoenosis the vegetation is fairly homogeneous, the investigator will often be in a single humus system composed of a hidden mosaic of humus forms. In the forest, this often depends on the appearance of and increase in the OH horizon (localized increase in the volume of litter, microconcavity, change of coverage or exposure), or conversely on the decrease until the disappearance of this same OH horizon.

(3) The questions which the investigator is called upon to answer are the following: (1) Is there an OH horizon? (2) How is the transition between the organic and the mineral parts of the humipedon? (3) Is the parent material (rock that directly or indirectly influences the formation of the diagnostic horizons of the humipedon) acidic or basic?

(4) What is the water dynamics in the profile and how long does a given horizon remain submerged? (5) Am I in a tidal zone? (6) What are the main living actors of litter biodegradation and why? (7) What is the importance of the impact of human action on the system?

(4) "Well-defined and easily recognizable" diagnostic horizons are associated to "central, typical" humus forms or systems. Cases of atypical horizons (but assignable to a diagnostic horizon defined by estimating the percentages of its components), or humipedons that mark the passage from one system to another, are common in geomorphologically and floristically varied environments. There is usually a dominant humus form, and others are in ecological corollary. Once the investigator understands how to work, it becomes an interesting game to interpret the dynamics of the forest soil.

To define all the variations of the "disturbances" that humipedon horizons may encounter is useless. We contented ourselves with describing those of wild mammals reported in Figure 7C,D), and which ultimately remain connected to the original natural horizons.

TerrHum: a way to standardize classification at the planet level.

Young Italian climbers investigated the humus systems that generate on the rocky mountain ledges, trying to understand the process of soil formation [67–70]. Other authors linked the humus systems to soil pollution [14,49], others to soil nutrition [71], biodiversity [72,73], or organic carbon content [74]. If nature and soil lovers began to classify humipedons in a coordinated and standardized way, it would be possible to map the morpho-functional state of the world's biotic soil. Management that respects the soil biodiversity would be much easier. Humans could even seriously plan far-sighted land use and mitigate global warming (Supplementary Materials 4).

Supplementary Materials: The following supporting information can be downloaded at: 1: Special Issues published in Applied Soil Ecology, 2018: Humusica 1–Terrestrial Natural Humipedons, https://www.sciencedirect.com/journal/applied-soil-ecology/vol/122/part/P1 (accessed on 27 June 2022); 2: Humusica 2–Histic, Para, Techno, Agro Humipedons, http://www.sciencedirect.com/science/journal/09291393/122/part/P2 (accessed on 27 June 2022); 3: Humusica 3–Reviews, Applications, Tools, https://www.sciencedirect.com/journal/applied-soil-ecology/vol/123 (accessed on 27 June 2022); 4: Video: Humipedon Critical Zone (Conference held on 28–29 September at IUFRO World Day—Digital Forest Science iForum 2021, and then renewed on 12 October 2021 at the Luxembourg Institute of Science & Technology) https://datacloud.tesaf.unipd.it/index.php/s/qMgtlYj1KeEJ2i7 (accessed on 27 June 2022).

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2.2 HUMUS DYNAMICS IN FOREST ECOSYSTEMS

Humus is not a static element in the forest ecosystem. In the 1990s, Bernier and Ponge (1994) pointed out that the described humus forms vary in the silvogenetic cycle of the forest and depend on the variation of plants and animals in the soil. This variation is biphasic and is considered fundamental to the forest regeneration process, and consists of a tree growth phase in which the humus gradually shifts from mull to moder with a progressive decrease in earthworm activity, and a tree maturity and decline phase in which a gradual return to mull and rich earthworm activity is observed. These findings have been confirmed in subsequent decades and complemented by new knowledge of forest dynamics.

The aim of the article entitled "Soil, Humipedon, Forest Life and Management" is to review the studies on humus dynamics in the forest regeneration cycle and to supplement them with new data in order to give a clear and complete picture of these dynamics and to provide a starting point for proper forest management. After an introductory part on the humipedon of mountain forests and its classification, an in-depth study is made on the evolution of humus systems during the silvogenetic cycle, with a special focus on the amphi system, which plays a fundamental role in alpine ecosystems.

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Review

Soil, Humipedon, Forest Life and Management

Roberto Zampedri [1], Nicolas Bernier [2], Augusto Zanella [3,*], Raffaello Giannini [4], Cristina Menta [5], Francesca Visentin [5], Paola Mairota [6], Giacomo Mei [6], Gabriele Zandegiacomo [3], Silvio Carollo [3], Alessio Brandolese [3] and Jean-François Ponge [2]

[1] Unità di Ecologia Forestale, Fondazione Edmund Mach, 38098 San Michele all'Adige, Italy; roberto.zampedri@fmach.it
[2] Muséum National d'Histoire Naturelle, CNRS UMR 7179, 91800 Brunoy, France; nicolas.bernier@mnhn.fr (N.B.); jean-francois.ponge@mnhn.fr (J.-F.P.)
[3] Dipartimento Territorio e Sistemi Agro-Forestali, Università di Padova, 35020 Legnaro, Italy; gabriele.zandegiacomodelugan@studenti.unipd.it (G.Z.); silvio.carollo@studenti.unipd.it (S.C.); alessio.brandolese@studenti.unipd.it (A.B.)
[4] Dipartimento di Scienze e Tecnologie Ambientali Forestali, Università di Firenze, 50133 Firenze, Italy; giannini.raffaello@gmail.com
[5] Dipartimento di Scienze Chimiche, della Vita e della Sostenibilità Ambientale, Università di Parma, 43124 Parma, Italy; cristina.menta@unipr.it (C.M.); francesca.visentin@unipr.it (F.V.)
[6] Dipartimento di Scienze del Suolo, della Pianta e degli Alimenti, Università di Bari, 70126 Bari, Italy; paola.mairota@uniba.it (P.M.); giacomo.mei@uniba.it (G.M.)
* Correspondence: augusto.zanella@unipd.it; Tel.: +39-0498272755 or +33-783615957

Abstract: In recent years, three sections (Humipedon, Copedon and Lithopedon) were recognized in the soil profile. It was then possible to link the first and most biologically active section to the characteristics of the environment and soil genesis. In particular, it is now possible to distinguish organic horizons, mainly produced by arthropods and enchytraeids in cold and acidic or dry and arid environments, from organo-mineral horizons produced by earthworms in more temperate and mesotrophic environments. Each set of horizons can be associated with a humus system or form, with important implications for forestry. Anecic/endogeic earthworms and Mull or Amphi systems are more abundant in the early and late stages of sylvogenesis; by completely recycling litter, earthworms accelerate the availability of organic and inorganic soil nutrients to roots and pedofauna. On the other hand, arthropods and Moder or Tangel systems characterize the intermediate stages of sylvogenesis, where thickening in the organic horizons and the parallel impoverishment/reduction in the underlying organo-mineral horizons are observed. Recognizing the humus system at the right spatial and temporal scale is crucial for the biological management of a forest. This article includes a data review, new data from a doctoral thesis, and recent comparisons of Italian and French investigations.

Keywords: humus; Humipedon; forest soil; forest dynamics; soil biodiversity; soil functioning; spruce forest

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1. Introduction

The purpose of this work is to provide practical information to forest managers that can be used to correctly interpret soil quality for silvicultural purposes. For this reason, it was divided into the following four sections and a conclusion:

(1) What is soil, and what, in particular, is forest soil?
(2) Soil classification
(3) The Humipedon in mountain and high-mountain forest environments
    - Bipolar Amphi
        - Bipolar Amphi generated by the destruction of Mull humus

        - Bipolar Amphi generated by the destruction of Raw humus
    - Forms of stable Amphi humus

(4) Humipedon and forest management
(5) Conclusions

The first two sections state some fundamental concepts that can be skipped by specialists who wish to start at the heart of the subject. In the third section, the topic is attacked operationally by identifying two sets of Humipedons that allow the reader to understand the natural dynamics of forest topsoil. After stating the elements of Humipedon classification, the fourth section mainly reports the results of a doctoral thesis. In it, the quality of Humipedon is investigated in targeted climatic and geological situations and at different stages of development in an alpine spruce forest. All readers can quickly find the main results for the finalized content of this thesis in the Graphical Abstract.

A reader who prefers images to text can understand the essential content of this article by reviewing the figures and their legends.

Although focused on spruce forests, this review should encourage readers to observe/study Humipedon in the forests they know or work in to better understand how these ecosystems use the ground to live and renew themselves.

2. What Is Soil, and What, in Particular, Is Forest Soil?

It is not easy to define what soil is [1–4]. Various aspects of this "object" still elude science [5]. In a functional context, we can say that soil is the "belly" of our planet Earth [6]. In fact, soil "digests" everything that falls on it and permanently recycles and stores everything. It is not yet clear how or what all the structures recycled over time become in detail, but the outcomes of this incessant digestion certainly support the natural evolution of the entire planet [7].

In the case of forests, a short focus can help to define what forest soil is from a descriptive and functional point of view and provide indications related to the needs of proper forest management [8].

From a physical point of view, in a forest, we walk on the ground: a "pabulum" (literally, "absorbable food") that soil scientists divide into "horizons". The following are clearly identifiable in the topsoil or Humipedon: organic horizons (of almost intact litter: OL; of fragmented litter: OF; of litter transformed into humus: OH; organic remains in water, almost intact: HF; half decomposed: HM; well decomposed: HS) and organo-mineral horizons (A from earthworms, A from arthropods, A non-zoogenic). Horizons that are very commonly used to describe other underlying parts of the soil include Copedon horizons (mineral, depleted: E; mineral newly formed: B) and Lithopedon (fragmented rock: C; compact rock: R).

Soil horizons are the result of an interaction between the geo-climatic environment in a geographical area on Earth and the organisms that are more or less permanently present in that volume of the biosphere (Figure 1). Many of these organisms complete their life cycle only in this component of the ecosystem. Although they belong to the same forest ecosystem, topsoil and soil have very different but complementary functions. They cannot exist without each other until the limit of their reserves is exhausted.

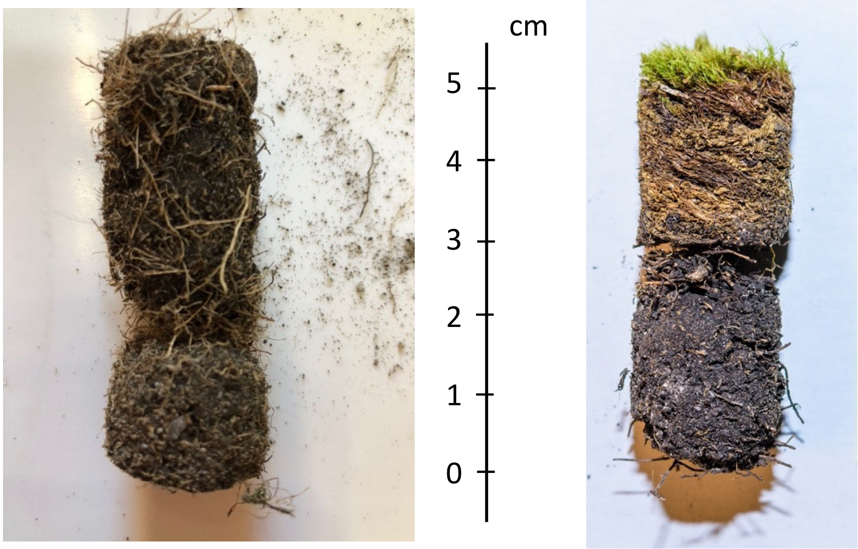


Figure 1. Initial soils on acidic (**Left**) and calcareous (**Right**) ledges sampled by two student mountaineers [9,10]. The centimeter scale bar shown in the center applies to both images. These profiles were obtained from vertical rock faces at an altitude of about 2000 m by driving a tube into the ground supported with ledges 50–150 cm wide. In the photo on the left, we can see the organic part matted with roots (OH), which is detached from the slightly lighter organo-mineral part (A) and resting on the rock; on the right, detachment occurs between a light brown organic part made of decomposing moss (OF) and a darker organic part in contact with the rock (OH). These micro-soils rested on a fragmented rock horizon that was not picked up with the probe (C horizon). These profiles illustrate the early stages of soil formation in an untouched, high-altitude environment. The diagnostic horizons are composed of arthropods and enchytraeids excrements, grains of fragmented rock and shredded and decomposed organic matter, owing to the action of bacteria and fungi.

The biological characteristics primarily concern biodiversity, which, in the soil, is clearly different from that out of the soil due to the lower presence of autotrophs and the dominance of a more complex network of heterotrophs. In terms of the number and variety of species and individuals, the soil biodiversity is richer than that outside of the soil [11–14].

Then, the storage function becomes important. Soil is the "living bank" of the forest system [15]. It receives energy and matter from the outside and packages it in storage and release structures that are sensitive to biological stimuli. It looks like a "living sponge" placed on the rock. It can be several meters thick under particularly favorable conditions. At our latitudes, the thickness of the soil is less than 100 cm. The seeds of most forest plants lie dormant in the soil. When environmental conditions are appropriate, which, depending on scale, can correspond to a stand-replacing disturbance (e.g., wind storm avalanche, fire, etc.) as well as to a gap creation (e.g., fall of individual old trees), the activities of soil's trophic network trigger the cessation of seed dormancy, and these seeds start the first dynamic phases of the forest ecosystem [16,17].

Finally, in soil genesis, Humipedon oversees the renewal and continuous growth of the forest ecosystem. In order to resist wear and tear and maintain an effective action over time, living organisms must undergo constant recycling. In a forest composed of complex and interconnected uni- and multicellular organisms, the natural death of these organisms involves the recycling of significant quantities of components that are transformed into the soil. This recycling takes place in two stages: decomposition of the original structures and composition of new structures ready for reuse inside and outside of the ground. The point is that both organic and mineral materials are concerned with the dichotomy between building and reuse fractions (also called inherited and newly formed). The inherited part of the soil is issued from dislocation, while the newly formed part of the soil generates fundamental materials such as clays and humic acids. The two opposing movements end at a point that is still not fully known today. This unknown is expressed in the word "humus", which has a transcendental meaning that always stimulated scientists. A milestone in this scientific journey is certainly the study by Miller and Urey [18]. They placed the molecules of a primitive soil soup in a test tube and, imitating the environment of a planet in its infancy, they attempted to create the first bricks of the living world. Using artificial electrical discharges mimicking distant storms, that primitive matrix produced many of the molecules that make up living cells.

It should be emphasized that soil is not a habitat. There is no "home for living organisms" called "soil" because soil microorganisms "are soil". An example of a soil habitat could be that of the moon as it does not contain microorganisms [19]. A "soil-habitat" can be made on our planet by sterilizing ordinary soil using autoclaving at 105 °C for 48 h. However, the problem is that once sterilized, it will no longer be soil. Soil made up of organo-mineral aggregates containing microorganisms looks more like a giant amoeba than an inert rock. It is certain that soil corresponds to an ecosystem [20], but to come to consider the soil as if it possessed the functional complexity of a supra-organism is still an open discussion [21].

The present article is based on a purely living soil definition. Some of the authors strongly disagree with a purely biological definition for the concept of soil, but we mutually agreed to keep it in this article to provoke discussion and growth. Thus, we focus on a fundamental issue that cannot remain unresolved: the soil is either a biological matrix and, therefore, it must be treated as such (it must be protected as an inherited living structure) or it is a raw material inhabited by living beings and, therefore, we can destroy and modify it (for example, with the plow or by occupying it without thinking that we are destroying something irrecoverable) as if it were not an entity with a valuable historical path and heritage.

To conclude this introduction to the concept of soil, we now discuss earthworms, which are the main "builders" of soil on our planet, at least in all areas between −5 and +35 °C [22,23]. Trying to summarize their action in a few lines is difficult. Therefore, we recommend downloading for free the fantastic book by Clive A. Edwards and Norman Q. Arancon [24], in which historical research on earthworms is collected, and reviewing the appropriate information. This book takes the reader very far and on the same path traced by Darwin in 1881 [25], in search of the functional and ecological significance of these underground animals.

3. Soil Classification

In general, to better understand and correctly use the components of nature, it is necessary to determine their classification. In the case of pedology, the fact that the conceptual difference between "soil-living-system" and "habitat" was fundamental has complicated the work of soil classification.

Historically, forest pedologists focused their research on describing and classifying natural or semi-natural soils that have not been manipulated by programmed human practices (unplowed). These soils show a vertical stratification (presence of horizons) because the addition of litter on the surface and the alteration of the bottom bedrock have contrasting effects on the soil profile. The mechanism underlying the biological integration of litter into the rest of the profile (first 30 cm) was described, distinguishing different degrees of biodegradation in this litter, which remains whole on the surface and then fragments until it becomes "humus" in contact with soil minerals [26]. The foresters found that these surface horizons varied according to the climate and biocenosis that incorporated the litter into the soil. Somewhat confusingly, one or all the surface horizons in forest soil were called "forest humus". Today, these surface horizons are classified into humus systems and forms.

Agronomists classified soils that were generally plowed to grow crops and produce food [27]. Periodically, the uppermost horizons in these soils were mechanically mixed with the underlying horizons to form a more effective matrix for cultivation. Thus, the artificial stratification at the surface was added to the deeper natural stratification. Agronomists were mainly interested in the chemical and physical properties of what they considered to be a growing substrate. Soil samples from the plowed layer (first 30–40 cm) could be obtained before and after cultivation and analyzed in order to balance and replenish the soil with fertilizers that cultivation had removed in the form of mineral elements. The living beings in the agricultural land were defined as useful, indifferent, or harmful according to their repercussions on production.

In the mineral horizons developing below the first 10–40 (just described), the biological aspects are less important and their composition and structure change less rapidly with time. Their chemical and physical characteristics (e.g., thickness, texture, pH, color) were divided into classes, as defined by the historical experience of specialists, and then related to each other to describe diagnostic horizons. Specific sets of diagnostic horizons were assigned to groups of reference soils with names (reference soil groups). Adjectives (qualifiers) were also used to improve the definition of the unit to which the observed profile belonged. The American school also considered climate [28,29], and the Russian school gave weight to vegetation [30]; however, for more than 30 years, the ecological and biological aspects of soil formation and dynamics were ignored in the volumes of the WRB for soil [31]. Luckily, a beautifully illustrated version of the WRB soil classification was recently published. In it, the planet's soils are finally represented within phyto-climatic bands [32].

In daily practice, scientists who need to know the name of a specific soil (some journals require the use of soil names) ask soil specialists to intervene. These specialists analyze the profile and provide a name. The information contained in the name of the soil is either difficult for the user to access or has a descriptive and impractical interest. By working on the balance of nutrients and organic carbon, or on the possible presence of a clayey and impermeable horizon at depth, agronomists and foresters are able to manage soil without the need for classification. Unfortunately, this has serious consequences. For example, agricultural soils have lost 80% of the organic matter they contained 50 years ago [33–35]. Organic matter is related to the energy stored in the soil and the water-holding capacity of the soil. We know that the loss of organic matter is due to a sudden decrease in biodiversity (related to the use of herbicides and pesticides [36,37]), which is a consequence of the little importance that has been given to this component in the diagnosis of soil quality [38].

Errors in the selection of forest plant species are often related to the fact that the soil is considered a product of the vegetation rather than a complex component of the forest ecosystem whose dynamics both depend on and influence the ecosystem's equilibrium state [39,40].

Recently, in an attempt to clarify and better understand the functioning of the forest floor [41], the "ecosystem-soil" (in the sense of [42–45]) was divided into three sections, functionally grouping the horizons as follows [6]: Humipedon (organic and organo-mineral horizons with biological determinant: O and A), Copedon (mineral horizons of recent formation: E, B) and Lithopedon (rock mineral horizons: C, R).

In the Humipedon, most of the biological activities of the soil take place because they are strongly dependent on the input of energy that comes in the form of organic molecules from the vegetable topsoil.

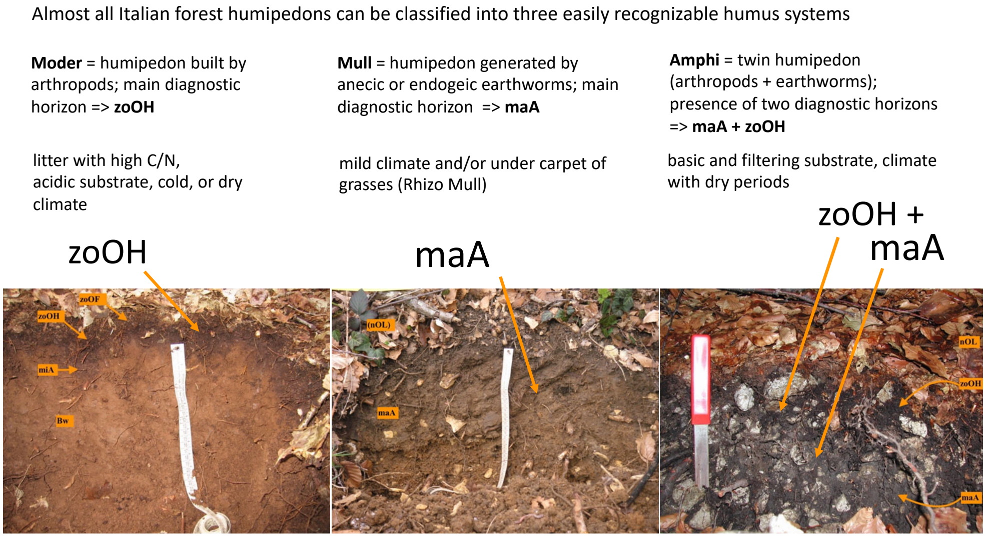
The Lithopedon is the deepest part of the soil, which is in contact with a rock that is transformed. In the Lithopedon, there are mineral blocks that disaggregate and contribute to feeding a flow of water and nutrients that circulate in the soil by gravity, capillarity, and biological ascent. In the central part, or Copedon, chemical–physical and biological processes take place that transform this boundary mass between the organic and mineral layers into something new (neo-clays, hydroxides, etc.) and suitable for composing the living sponge that is the soil as a whole.

The classification of Humipedon (Figure 2) is both biological and morpho-functional. It is based on the principle that the diagnostic horizons that make it up are the result of biological activities visible to the naked eye in the field. Specific series of these horizons define humus systems that develop in ecologically limited natural environments. The relative thicknesses of the diagnostic horizons define the humus forms within each humus system.

Copedon corresponds to the E and B horizons in soil classification. It is not yet classified as a biological ecosystem soil.

The classification of Lithopedon reconsiders the whole of the C horizon and the R substrate of the soil, proposing units related to the functioning of such deep parts of the soil [46].

The Humipedon is studied in more detail than the whole soil because foresters and agronomists know that it is very important for the biological and dynamic aspects of soil. Although it does not appear in the international soil classifications cited above, more recent emphasis has been placed on soil biology to improve the agricultural use of Humipedon. The sustainable agriculture policy (which is part of the very recent European agricultural development plan) considers and promotes Humipedon using studies on the biological quality of soil carried out separately and equally well for arthropods and earthworms [47–50]. Fortunately, these practices are tending to spread and establish themselves internationally, superseding areas that were dedicated to intensive agriculture [51–53]. Among other things, attempts are made to imitate nature by reducing the work of the soil on the surface, respecting the natural biological stratification of the soil [54–57], and recovering the biodiversity and organic matter that was lost.



Almost all Italian forest humipedons can be classified into three easily recognizable humus systems

Moder = humipedon built by arthropods; main diagnostic horizon => **zoOH**

Mull = humipedon generated by anecic or endogeic earthworms; main diagnostic horizon => **maA**

Amphi = twin humipedon (arthropods + earthworms); presence of two diagnostic horizons => **maA + zoOH**

litter with high C/N, acidic substrate, cold, or dry climate

mild climate and/or under carpet of grasses (Rhizo Mull)

basic and filtering substrate, climate with dry periods

Figure 2. Italian forest Humipedons are mainly attributed to three humus systems: Mull (from earthworms), Moder (from arthropods) and Amphi (from earthworms and arthropods). The latter was first recognized by Franz Hartman 50 years ago. He called it twin humus. In 1995, the French considered it as a strange Mull and named it Amphimull. By 2018, it regained full recognition as a fundamental unit of classification, with the definitive name of Amphi (=double, twin). With this humus system, it is much easier to understand the short-term dynamics (years, decades) of soil linked to the dynamics of the forest and its structural types.

Foresters, on the other hand, improve the description of the superficial diagnostic horizons and consolidate references to the different environments in which soils are generated. The overall picture is very well organized, with precise links to the understanding of soil functionality, taking under consideration the carbon cycle, the dynamics of mineral elements and litter, the relationships with natural topsoil renewal and soil changes in the structural phases of the forests [58].

4. The Humipedon in Mountain and High-Mountain Forest Environments

The strength of the interactions within a couple can be tested at their limits. This is as true for the interactions between two human beings as it is for the interactions between vegetation and humus. Ponge et al. [59] postulate that at the low-montane level, forest regeneration is limited most of the time by light alone because humus metabolism is always high; in contrast, at the high-mountain level, light becomes less and less of a limiting factor and humus becomes thicker. As a consequence, the role of burrowing animals such as earthworms in ecosystem functioning changes from important to critical as the transition from mountain to subalpine forest occurs. Earthworm burrowing activity alters humus on two levels. Macroscopically, the large anecic earthworms are able to modify their environment by spreading their organo-mineral feces along their main middens and secondary exploratory tunnels. Microscopically, earthworms ingest both organic and mineral material, mixing the two thoroughly. The result of their activity is thus the formation of the organo-mineral complex [60–62]. As a result of the increasing rate of organo-mineral complexes near the surface, tree seeds can easily find a favorable microsite to grow. André et al. [63] show that a key component in forest regeneration is the occurrence of mineral substance near the surface (Figure 3). In an experimental plot in Savoy, almost all very young spruce trees were found to be growing on mineral deposits created with the burrowing activity of small mammals compared to the undisturbed soil [64]. This regeneration micro-niche could be experimentally replicated by stripping the holorganic part of the humus.

In the subalpine belt, there are many reasons why minerals come close to the surface. The most effective is indeed the burrowing of earthworms (Figures 4 and 5, in Section 4.1), but it can also be the consequence of other biological activities as diverse as wild boars [65], tree uprooting [66,67], millipede activity [68], small mammals [69] and human digging of forest roads [65,70]. It can also have a physicochemical origin, such as an alteration to the bedrock of a small overhanging cliff and the subsequent debris on steep slopes. All these are drivers of humus form change, leading to a mineral enrichment near the surface that supports forest regeneration. However, such mineral input in a holorganic humus form is often discontinuous in space and time, or, if bioturbation is generalized, it is present at low levels in subalpine forests [71]. In contrast to lowland forest bioturbation, which produces the Mull humus form, low-level and/or episodic bioturbation in mountain environments produces a range of Amphi humus forms.

The four Amphi humus forms (Leptoamphi, Eumacroamphi, Eumesoamphi, Pachyamphi), identified in the Amphi humus system using the thickness of the OH horizon and the structure of the A horizon [6], can be grouped into two main functional categories. The Bipolar Amphi forms evolve continuously between the Mull and Moder or Tangel humus forms, sometimes in the direction of Mull and sometimes in the direction of Moder or Tangel. They are characterized by the perturbation of large earthworms, which release their biomacrostructured organo-mineral excrements into the organic layers, orienting the evolution in two opposite directions: toward Mull (Leptoamphi) when the excrements increase and toward Moder when instead they decrease (Eumacroamphi, with thicker OH). The Stable Amphi forms are stable intermediates between Moder or Tangel and Mull, reflecting an incomplete but homogeneous organo-mineral incorporation. They generate a holorganic horizon above (OH) and a biomesostructured or a mixed biomeso- and biomicrostructured organo-mineral horizon (meA) below (Eumesoamphi, or Pachyamphi with thicker OH).

In general, with an increase in altitude, the Humipedon passes from Mull to Moder and finally to Mor (rare in a forest environment on the Italian side of the Alps) on an acidic substrate, while it passes from Mull to Amphi and then to Tangel on a calcareous or dolomitic substrate. The difference between a very thick Dysmoder and a Mor or a Tangel is a specialist topic and requires knowledge related to soil fauna. To simplify presenting the dynamics of the Amphi in the following paragraphs, we prefer to use the name Raw humus for Moder, Mor and Tangel, in which anecic earthworm bioturbation is absent. We can say in a simplified way that we progressively pass from Mull to Raw humus with a rise in altitude due to a decrease in the biological activity of the soil. This dynamic is important for understanding how forest soil works. Below we propose a practical simplification that could facilitate an understanding of Humipedon in a mountain forest environment even for beginners.

Figure 3. Examples showing subalpine forest regeneration sites on a scree slope. (**Left**): on weakly stabilized skeletal soil. (**Center**): the few-centimeters-thin A horizon of a Mull system on skeletal soil on and between blocks of rock in Grand Follié forest—1550 m, Saint Foy Tarentaise, France. (**Right**): on a stump, i.e., an example of a 50 cm thick Ligno humus form (Somadida forest—1300 m, Auronzo, Italy).

4.1. Bipolar Amphi

4.1.1. Bipolar Amphi Generated with the Destruction of Mull Humus

As Mull activity weakens, the first stage of Amphi is characterized by a more or less continuous OH horizon, depending on the drastic or progressive collapse of earthworm activity, overlaying a well-developed A horizon (Figure 4). As the bioturbation of Mull humus weakens, the humus develops an OH horizon with a sharp transition to the underlying A horizon. Initially, the OH layer is thin or in pockets and the A horizon is well preserved, so the humus form is a Leptoamphi. As time passes and the burrowing activity decreases, the OH layer develops, the A horizon loses its structure and the humus becomes an Eumacroamphi. Such Amphi humus forms are particularly observed under young spruce when mull-forming factors such as large anecic earthworm activity collapse [72] (Figure 5, Left, Section 4.1.2).

Figure 4. Example showing Bipolar Amphi. Below this nucleus of Pinus cembra, a simple and stratified structure of the Humipedon can be clearly seen, with relatively thin organic OL and OF horizons on the surface resting on a dark and organic OH horizon. The Humpideon distinguishes itself from the underlying and lighter organo-mineral horizon A (on the pedologist's hand), which is biomacrostructured by earthworms. Monte Penegal, Trentino, the Alps, Italy.

4.1.2. Bipolar Amphi Generated with the Destruction of Raw Humus

The recent burrowing activity of a new earthworm community, in a raw humus context (often a thick Dysmoder), drives the humus profile to drastic changes (Figure 5, Center and Right). Earthworms nourish the entire humus profile with sparse but substantial dropping activity (from the OL layer to the A/C soil horizon to the OH layer) (Figure 4, Center and Right). Both the dispersal of organo-mineral feces and the depletion in OL horizon material cause the bipolar Amphi to exhibit some new features within the OL, OF and OH horizons. Early in the process, the A horizon is nearly absent, and then biomacrostructured organo-mineral complexes of anecic worms are distributed along the OL, OF and OH horizons. Over time, the A horizon develops and the OH horizon becomes discontinuous and relict (Figure 5, Right). The soil under old trees hosts a new population of earthworms as the trees age and prepare for their replacement [72].

Notice that these Bipolar Amphi (Sections 4.1.1 and 4.1.2), generated from the destruction of Mull or Raw humus, are not symmetrical. The first is characterized by the establishment of stratification with a sharp transition between horizons. The second instead shows the transformation of each humus horizon due to the stochastic deposition of new earthworm casts. This phenomenon could be interpreted as a hysteresis process related to the long-term life cycle of a forest ecosystem exposed to a harsh climate. Such Bipolar Amphi humus forms may qualitatively and quantitatively deviate from the range of thickness and compositional variations established in the current humus classification systems [6]. In these environments, and connected to forest dynamics, the principle of coexistence typical of the Amphi undergoes a vertical disruption: one of the two systems is no longer above the other, but they coexist patchily, leading to the mixed cohabitation of OH and A horizons that characterizes Bipolar Amphi. We recommend recording these new mixed horizons as AOH or OHA, depending on the dominance of the first or second component of the mixture.

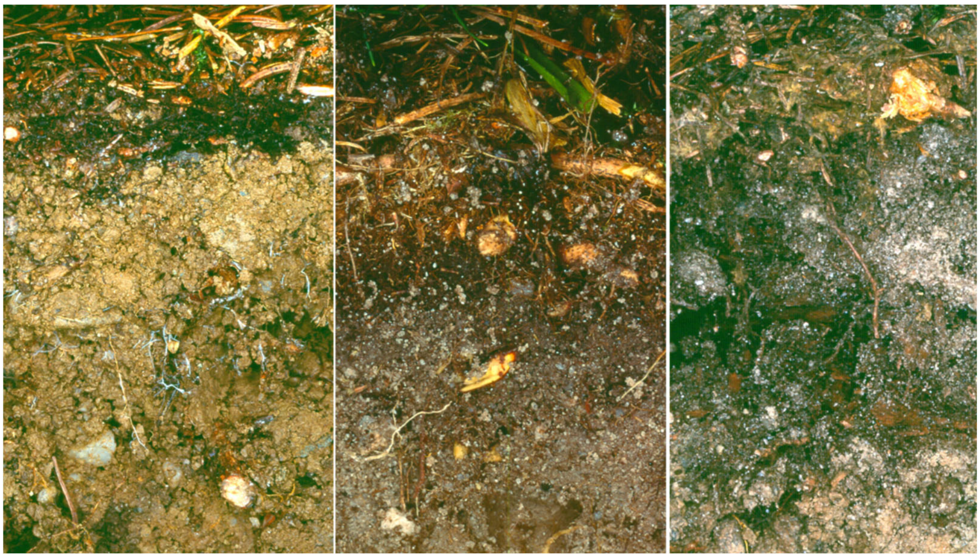


Figure 5. Bipolar Amphi humus form. (**Left**): Bipolar Amphi (destruction of a Mull, starting process) under a young regeneration spruce tree with three distinctly separated horizons: OL, OF lying above a dark discontinuous organic OH and deposited above a well-developed gray glomerular A (Mâcot-la-Plagne forest, 1550 m, France). (**Center**): Bipolar Amphi (destruction of Raw humus) under an old larch tree showing the dropping of organo-mineral earthworm casts along the profile, which disturbed the structure and destroyed the clearly separated horizons in the former Dysmoder (Mâcot-la-Plagne forest, 1550 m, France). (**Right**): Bipolar Amphi (destruction of Raw humus) under an old spruce tree showing advanced destructuration of the OF and OH horizons with the inclusion of earthworm organo-mineral casts (Mâcot-la-Plagne forest, 1750 m, France).

4.2. Stable Amphi Humus Forms

Stable Amphi is either a real intermediate humus form or the superposition of the two humus forms. In the first case, as a real intermediate between Raw and Mull humus, the drastic transformation of the pre-existing OF and OH layers (or A horizon) into a mixed OHA horizon reflects an incomplete but well-distributed organo-mineral incorporation (Figure 6). In these Amphi forms, the bioturbation force is continuous but at a low level; it does not completely mask the stratified organization of the Raw humus form (organic horizons are still in place) as it occurs in Mull systems, where holorganic horizons are absent. The result is a thick OHA humus horizon, i.e., an OH horizon containing a substantial fraction of minerals. In Stable Amphi, the bioturbation force is often weaker than in Bipolar Amphi. In contrast to Bipolar Amphi, which are generally biomacrostructured (composed of large aggregates with a diameter >4 mm), Stable Amphi show biomesostructured (1 mm < aggregates $\leq$ 4 mm) or even biomicro (aggregates $\leq$ 1 mm) A or OHA horizons since the forces of bioturbation depend on tiny organisms such as enchytraeids, small epigeic earthworms, diplopods or simply passive mineral input during weak but persistent landslides. The weakening of bioturbation forces is generally associated with harsh climates (cold mountain and subalpine forests and seasonally dry and warm submontane forests) [71,73]. Amphi humus with an A horizon endowed with biomeso- and biomicrostructured A or OHA horizons has also been observed in Mediterranean environments [74,75]. We think that in these environments, the low temperature would not be a limiting factor, but periodic droughts might have an effect.

In some very specific cases, we can observe the cohabitation of endogeic fauna with an epigeic fauna. The resulting humus profile is twofold. On the one hand, there is the typical sequence of layers, i.e., OL, OF and OH, inherited from the Moder form. On the other hand, there is a biomacrostructured A horizon similar to a Mull form. Both cases have very few interactions, leading to a stable and stratified Amphi humus form [76] (Figure 6).

Forest regeneration is the main driver of the Bipolar Amphi system, limiting the duration and the extent of Mull humus to old-growth eco-units and clearings [72]. This does not mean that Bipolar Amphi has nothing to do with climate, although it is possible to find a similar limitation in lowland forests [77]. However, the regeneration niche does not exactly coincide with the Mull or Amphi systems because of the beneficial role of decayed wood [78]. At the subalpine level, decayed wood is the main regeneration niche when mineral bioturbation is not possible [79]. However, decayed wood is not always visible as a large stump, log or trunk (Figure 6). More than half of the decayed wood is invisible at first sight because it has been incorporated into the humus profile over time [80] or because it comes from the decomposition of dead roots (Figure 7). As an analogy to Mull and forest regeneration relationships in the mountain zone, Ligno humus systems [81,82] are important for lowland and mountain forest regeneration and crucial in the subalpine zone. This is because real Mull and Amphi humus forms are rare, and the humus dynamic process is less and less efficient at activating bioturbation in preexisting Raw humus forms. Therefore, decayed wood is the last option for forest regeneration and becomes a key component in forest stability near the upper-forest limit [83].

The photographs in Figures 7 and 8 and the schematic representation in Figure 9 show how the wood in the forest is integrated into the soil, which becomes a resource for the future of the forest, considering, for example, the context of an Amphi system.

Figure 6. The Stable Amphi humus. (**Left**): The Amphi of a holm oak forest in Sardinia compared with equivalent Alpine Amphi. (**Center**): Amphi under a thin layer of red litter (larch needles, OL) composed of a reddish organic paste (OH horizon) mixed with large dark gray organo-mineral aggregates (A horizon) whose volume increases with depth (Val Tellina at 1800 m, Italy). (**Right**): Amphi restricted to the newly created OH/A layer, composed of an intimate mixture of holorganic brown droppings (OH, brown; more visible because it is less mixed towards the surface) and organo-mineral feces (A horizon) of small size (probably from small earthworms and enchytraeids), which are barely distinguishable (they are a little grayer and more compact toward the middle of the photograph) and become more mineral and grayer toward the bottom (Grand Follié forest, Sainte-Foy-Tarentaise, France).

Figure 7. Examples of Ligno humus forms from Grand Follié forest, Sainte-Foy-Tarentaise, France. (**Left**): a decaying stump with a young spruce tree in a pure wood humus form. (**Center**): a Ligno Dysmoder with a deeply sunk ligno layer, probably derived from a large decaying root. (**Right**): a complex Ligno Amphi humus form. Basically, such a profile corresponds to ancient Dysmoder or Mor humus forms that underwent two periods of mineral enrichment: the deeper half-buried one, probably generated from a landslide, and the second just below the OF layer, probably the fruit of biological enrichment. The whole profile develops over a decaying woody layer (Grand Follié forest, Sainte-Foy-Tarentaise, France).

Figure 8. Bipolar Amphi are common in spruce woods and show reddish layers of woody horizons; the deeper they are, the more they are decomposed. When the A horizon becomes dominant, the forest is ready for regeneration. Somadida forest, Belluno, Italy.

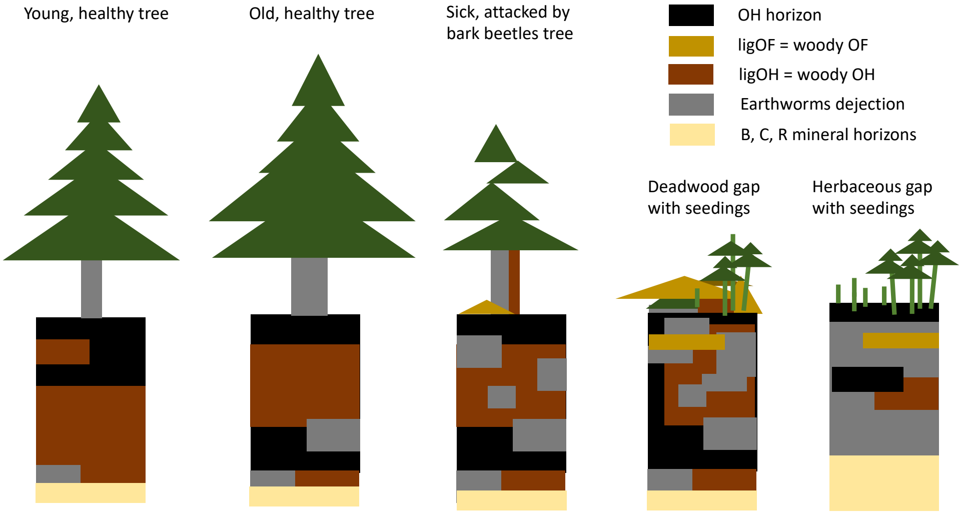


Figure 9. Humipedon dynamics (Zangiacomo, unpublished scheme still under investigation). In the Italian Alps, the bark beetle is currently attacking the Somadida forest (Belluno). We are trying to understand what happens at the Humipedon level. Trees lose their crowns (in the center of the figure, the tree that has lost part of its crown), and large quantities of bark and dead wood accumulate on the ground, feeding the Humipedon. Given the important role of decomposing wood (ligOF and ligOH horizons [81,82]), the dynamics could also be understood as a transformation from a Ligno system toward Amphi, perhaps slowing down the process that goes from Raw humus to Bipolar Amphi (third and fourth profiles, from the left) or Mull (fifth and last profile on the right), mentioned above.

The death of the trees is not a loss to the forest; instead, the actual functioning of a forest ecosystem and its biodiversity is hindered by the lack of decaying wood [84]. Like all other organisms that die, decaying trees feed the soil, which returns this organic matter after having been transformed into building blocks for a new complex part of the forest. We are currently comparing the morphological characteristics of Humipedon found under trees attacked by spruce bark beetles and under healthy trees (Figure 9). As the forest opens up due to the loss of canopy cover, the Humipedon receives more light in addition to the dead organic matter. The above-mentioned change in the Humipedon is triggered by the arrival of earthworms, which cause the integration of organic matter into organo-mineral aggregates and the progressive disappearance of OH horizons. This phenomenon can be observed with the naked eye in the forest. With the arrival of bark and wood from dead trees, the conditions of Humipedon resemble those found near old stumps. These conditions are known to stimulate forest regeneration (Figure 9).

5. Humipedon and Forest Management

An imaginary horizontal surface located below the forester's feet divides the forest into two distinct yet integrated and highly interacting components of the same ecosystem. In general, the aboveground component is better known because it is more accessible for surveys and measurements. This component transforms solar radiation into a more useful form of energy thanks to the photosynthetic process, from which the forester extracts a part of the biomass for the needs of the human economy. Under the forester's feet, a second "biological forge" develops the Humipedon. This also corresponds to a living, functional and efficient ecosystem component that supports and cooperates with the one above, from which it in turn receives the energy and matter needed for its distinctive processes, in the form of necromass (leaves, needles, bark, wood, the transformed remains of animals).

Therefore, Humipedon has its own ecological pyramid at different levels. Among the most typical animals in this ecosystem component, earthworms play a particularly important role as they feed on necromass along with the mineral soil. In their guts, which are almost as long as their bodies, they digest leaves and extract energy and minerals required for their metabolism. During this digestion process, part of the resulting molecules ends up in circulation in the earthworm's body, which provides the energy and matter required to complete its life cycle. The waste pulp expelled from the body of earthworms is what Darwin (Figure 10) discovered back in 1881 and called "soil" [25]. It helps us to imagine an elastic and living tube, which moves in the soil by ingesting leaves and earth and expelling "living-soil". This phenomenon became even more interesting when Marcel Bouché discovered that earthworms also eat their own excrement [85]. It is not ingested fresh but only after the excrement has matured in the soil for a certain period of time. Earthworms can extract matter to live on from their own excrement, and during the process, they move the soil unceasingly, making it homogeneous. Undisturbed in the forest floor, year after year, earthworms increase the amount of carbon in the Humipedon and distribute it uniformly in the profile. Furthermore, their movement creates tunnels in which air and water can circulate, allowing the degradation of organic matter and the reproduction of organisms present in the depths. Thus, the Humipedon can be thought of as an "auto-recharging living battery" of the forest. The recycling of organic matter produced by the autotrophs on the surface depends on earthworms, which continuously recharge the Humipedon "organic battery" of the forest. On a small scale, the presence of innumerable microorganisms can explain the functioning of the entire ecosystem, which evolves almost autonomously, because it should contain all connected living things, including humans, whether they are forest operators or not (Figure 10) [86,87]. We now return to the concept of *soil* (Chapter 1): *soil* (and even more, its most living part, the Humipedon) should not be considered a "habitat". Only the "new soil" that is "made by the living", "the organo-mineral sorption complex, the living things that make it and maintain it, the connection network between livings that keeps this network alive" is *soil*. The rest can be considered habitat or substrate. Either the soil is alive, or it does not exist [88–93].

Earthworms characterize Mull Humipedons, which develop in temperate, mild, warm and humid climatic environments, such as those found in the meadows described by Darwin, and in all the deciduous lowland forests in Europe. They do not have the OH (humiferous) horizon typical of colder or drier environments with conifers or xerophilous species. Other animals (enchytraeids and/or especially arthropods) are responsible for recharging the battery of the soil in these colder or even drier environments, such as the Mediterranean [94]. More generally, also considering wetlands, living organisms and the mechanisms for recharging and maintaining energy in the soil have evolved for each ecosystem environment (Figure 11).

There are freely available iOS (https://apps.apple.com/us/app/terrhum/id1366575503, accessed on 24 June 2023) and Android (https://play.google.com/store/apps/details?id=fr.inra.terrhum&hl=en_US&gl=US, accessed on 24 June 2023) applications in Italian, French and English languages, for tablets and mobile phones. During field observations, these applications can provide quick and useful indications for classification and photographic examples of horizons, forms and systems of humus.

From what has been said, we must conclude that it is necessary to plan and practice specific management for forest soil. When you walk on the forest floor, your feet are resting on a very useful living sponge, which exists not only as a support for the static anchoring of trees, which play a dominant role as the driving force of the ecosystem, but also as a source of energy for all the whole forest life.

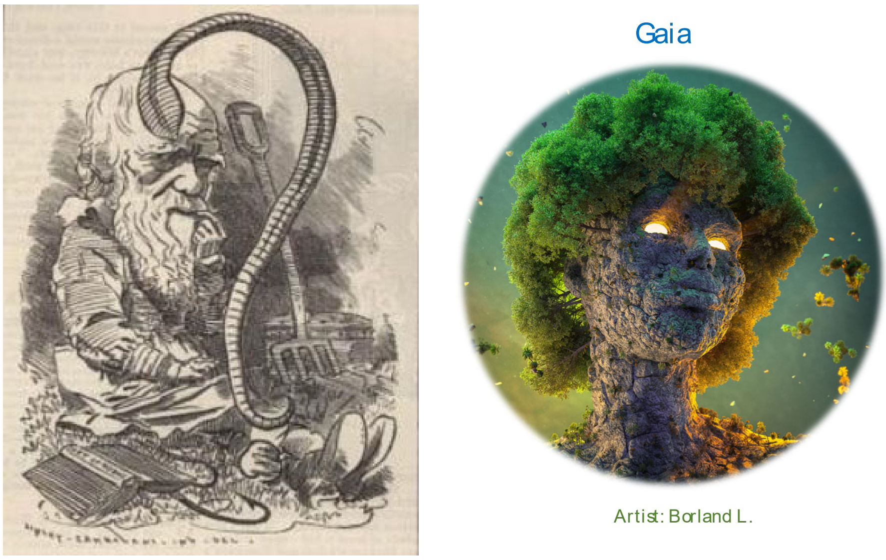


Figure 10. (**Left**): Linley Sambourne's satiric portrait of Darwin, published in Punch, 1881 (Punch's funcy portraits n. 54: https://www.meisterdrucke.fr/fine-art-prints/Edward-Linley-Sambourne/1045006/Charles-Darwin-%281809-1882%29-Naturaliste-anglais.-L%27%C3%A9volution-par-la-s%C3%A9lection-naturelle.-Caricature-d%27Edward-Linley-Sambourne-%281844-1910%29-dans-la-s%C3%A9rie-Fancy-Portrait-de-Punch,-Londres-1881,-ann%C3%A9e-o%C3%B9-Darwin-a-publi%C3%A9-The-Formation-of-Vegetable-Mould-through-.html, accessed on 24 June 2023). Note that the earthworm was depicted as a question mark, with its flattened tail mimicking the head of a potentially dangerous cobra. (**Right**): James Lovelock's Gaia is a scientific hypothesis only for blind scientists. We like to present Lokio Borland's captivating depiction of Gaia (https://lokio.artstation.com/projects/zgxJD, accessed on 24 June 2023) alongside the historical and dubious, but still modern, Darwin.

It is necessary to manage the soil, as already performed for the overlying tree part of the forest ecosystem, and to foresee a real plan for the conservation and restoration of the soil. This includes (i) an estimation of the average amount of organic carbon present in the soil in each management unit (above soil provision) and the structure and consistency of the eco-units (structural types in the sense of [95,96]); (ii) identifying the systems and forms of humus dominant in each eco-unit; and (iii) creating a list of functional groups of soil animals with the number of individuals in relation to seasonality [84].

It would be also of great interest to obtain a list of Humipedon living organisms, using sequencing of the soil metagenome ("Shotgun Metagenomic Sequencing"), to understand which functional groups of microorganisms are present in the soil and their relationships with topsoil plant species and with the other living organisms in the ecosystem [89,97,98].

It has long been known that vegetation structural types have their own Humipedon related to the age of the trees and the forest cycle [72,76,79]. A coordinated balance between the above and below ground is necessary for continuity in the forest cycle with a phase for consumption of soil resources in the young forest phase and replenishment and recapitalization of resources during the mature and final forest phases [99,100]. Knowing how to distinguish earthworm horizons from the others in Humipedon (Figure 2) allows us to check whether the evolution of Humipedon follows harmoniously that of the topsoil and to diagnose problems related to regeneration [101–103].

Figure 12 shows, as an example, the results of a doctoral thesis carried out in Trentino spruce forests [99]. It shows how the stages of forest development (herbaceous opening, natural regeneration, intermediate age, adult/mature forest) correspond to Humipedons classified in different humus systems. Such systems are shown schematically in Figure 12: Mull and Amphi (mainly Bipolar) humus are characterized by an A horizon formed by earthworms, which is not present in Moder or Mor humus. Basically, the forest floor evolves with the age of the trees it supports in balance with their needs. We consider that at the end of their life, trees prepare the soil for the next generation, feeding it and attracting the earthworms that prepare the organo-mineral aggregates that guarantee a good supply of water and nutrients to the new trees.

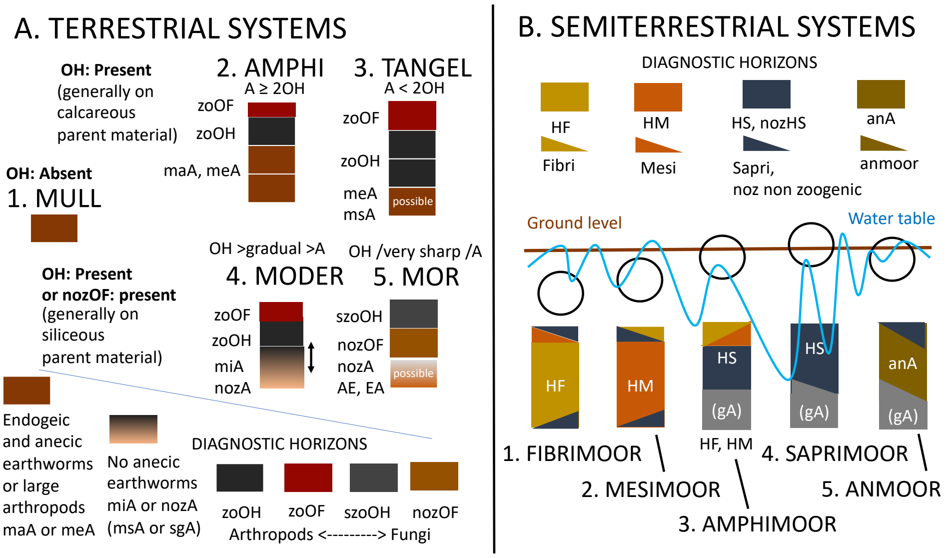


Figure 11. Synthetic keys for the classification of Humipedons in reference humus systems for terrestrial environments (non-asphyxiated soils) or for semiterrestrial environments (more or less submerged soils, peats). Modified from Zanella et al. [6] with permission. These keys are based on the recognition of diagnostic horizons. The superimposed set of these horizons corresponds to a function of the Humipedon, in harmony with the rest of the soil, with the vegetation and climate of those environments. Summary legend: Horizons of Humipedon: **Terrestrial** (aerated) organic horizons: OL, OF, OH + organo-mineral horizons: A; **Semiterrestrial** (more or less submerged) organic horizons: HF, HM, HS + organo-mineral horizons: A. Meaning of lowercase letters applied as prefixes to diagnostic horizon codes: zo = zoogenic, noz = non-zoogenic, szo = weakly zoogenic, an = of Anmoor, ma = biomacrostructured, me = biomesostructured, mi = biomesostructured, ms = massive, sg = single-grain. Meaning of the initial part of the name of semiterrestrial systems: Fibri = generally submerged and very fibrous, Sapri = completely transformed into organic pulp, Mesi = transition between Fibri and Sapri, Moor = peats. About the relative thicknesses of the horizons and the accuracy of the transition between them: A ≥ 2 OH: thickness of the A horizon ≥ 2 times that of the OH; A < 2 OH: thickness of the horizon A < 2 times that of the OH; OH < gradual A: gradual transition between OH and A, inaccuracy > 5 mm; OH/net/A: sudden transition between OH and A, inaccuracy < 3 mm.

The four stages of a forest can be clearly seen in the yellow–green–orange–blue sequence in Figure 11. All the data used in the analysis are summarized in Table S1, which is available in the Supplementary Materials. In the upper right corner of the PCA plot, we have the northern (BN) and southern (BS) basic spruce forests, in contrast to the AN and AS acidic ones in the lower left corner. The basic ones would have higher pH, % of exchangeable bases, thickness of A horizons and average temperature in May (y-axis on the left). On the other hand, the acidic north environments show decidedly higher values of CO, thicknesses of the organic horizons and miA horizons, and absolute minimum temperatures in January and in the spring and fall (y-axis on the right). On the left of the x-axis, high values for the average temperature in the first 10 cm of soil are observed in all seasons, corresponding to both acidic and basic southern exposures. Interestingly, and probably true, is the pH compensation with AS versus AN exposure, with a soil cycling becoming similar to that encountered in BS. When this does not happen and the climatic conditions are harsh (north exposure in both cases), the two phytocoenoses separate on the basis of the parent rock, and the soil cycle that takes place in the BN is very different from that in the AN (absence of Mull and presence of Mor).

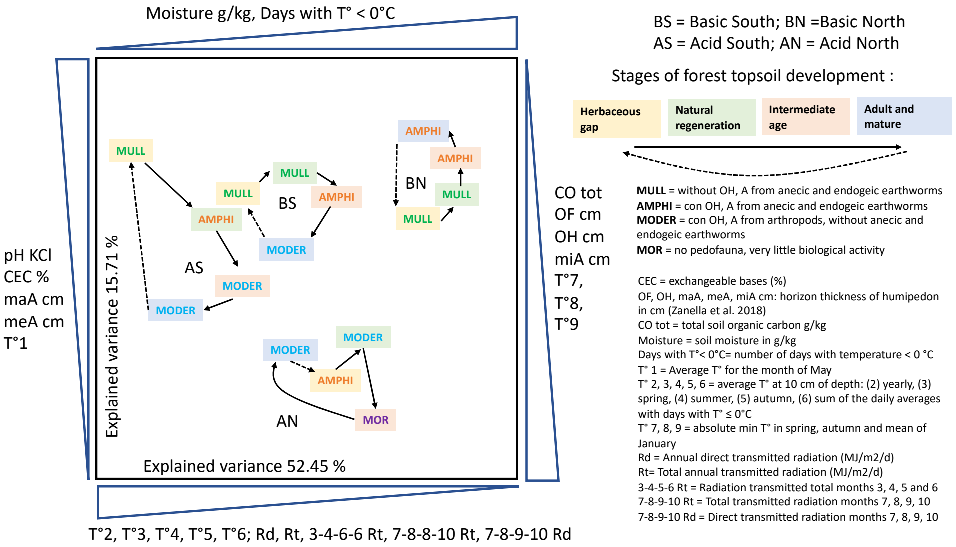


Figure 12. Humus systems in the development stages of an uneven spruce forest in acidic environments, facing south (AS) or north (AN), or in a basic environment facing south (BS) or north (BN). Notice how the humus system changes cyclically. In the Amphi and Mull systems, there are earthworms (with A horizons similar to those of the home garden); in the other systems, the earthworms are replaced with enchytraeids and arthropods, which form much more organic horizons, similar to those of shredded tobacco. The variance explained by the model presented on the plane of two axes (whose principal components are listed with increasing or decreasing importance along the axis) is about 68%.

An important consequence of this diagnosis, i.e., the fact that the forest floor has a life cycle linked to that of the aerial part of the forest, is that it must be taken into account in the management and felling plans. The soil cycle must also be respected. If the ground is a bank, and if for 100–200 years, the aerial part has been borrowing energy and minerals from the ground, then it is imperative that this loan is repaid with interest to the soil before spending continues. A first management guideline could concern not only respect for some monumental trees [104] and habitat trees [21,105] but also a decisive lengthening of the life of forest trees using a doubling the duration of the cycles currently practiced. It is very probable that old age trees mainly nourish the soil, preparing it for renewal [106,107] (Figure 9).

6. Conclusions on the Importance of Humipedon in the Sylvogenic Cycle of the Forest

It is necessary to preserve and feed the Humipedon to keep the forest healthy. Theoretically, this would mean returning to the forest a quantity of organic matter equal to that exported with the forest management plan. Since the raw material wood represents an irreplaceable asset, it is necessary to define the part of the annual woody biomass increment that should be returned with the awareness that in doing so, we are impoverishing even the soil system. Trees such as spruce can live 300–400 years or more if they are not cut down. Considering that spruce trees can be removed after 100–200 years, this means reducing their life expectancy and activity in the forest by half. For the soil cycle, this means losing all the return on the investment that was made in the aerial part of the forest. We know little about what happens in the soil during this second part of the cycle. The relationships between the trees and the living things in the soil change with old age. We know that this food web changes over time because the form or the system in which Humipedon is classified changes. We know that this evolution favors the reconstitution of the soil and the natural renewal of the forest. Missing this stage could damage the forest in the long run, just as soils were depleted with intensive post-World War II agriculture.

It is necessary to respect the soil in harmony with the observance of the rights of a living forest ecosystem. This means considering the functioning of the forest at the level of all phases of its cyclical development, which follow one another in the long term from renewal to senescence.

Finally, it is essential to strengthen research and disseminate knowledge on the functioning of forest soils. Figure 13 shows a green earthworm, and in Italian, it is said that "green is hope".

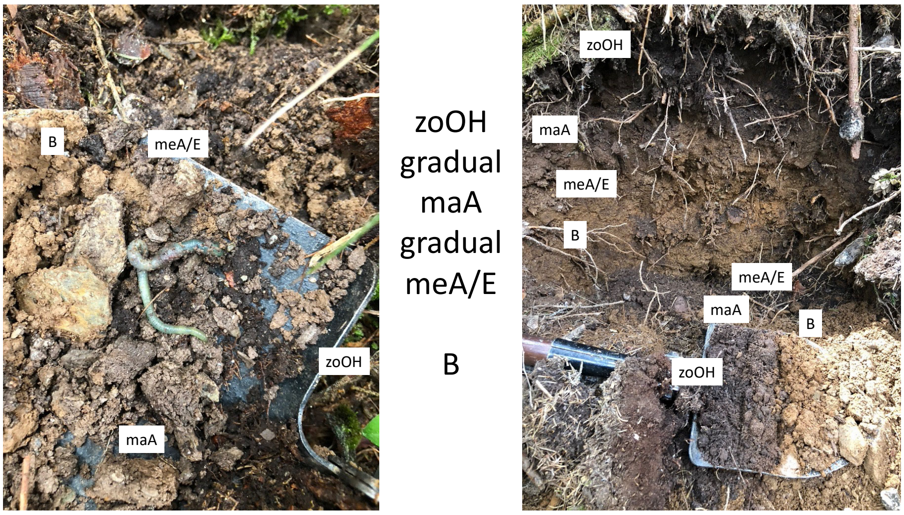


Figure 13. (**Left**): *Allolobophora smaragdina* in the organo-mineral horizon of a Bipolar Amphi (Dysmoder t->Mull) in a mixed fir forest in the Parco dei Sogni (Dream Park), Lorenzago di Cadore (Belluno). Foresters told us that Karol Józef Wojtyła (a Polish Catholic pope) came to walk and meditate in this park, and this is the reason why earthworms have a hopeful green color in these woods. It could also be that they are green because they follow humans [85] and they too want to change their fashion every now and then. (**Right**): The Humipedon in which this earthworm was found. It was resting between the OH and A horizons, where it was likely turning a Dysmoder (with thick OH and A/E horizons) into an Amphi (still with a Moder zoogenic zoOH, but with a new biomacrostructured maA typical of a becoming Mull). The mineral horizon B of Copedon is distinguished from the overlying meA/E or maA by the ocher color due to the iron oxides and by the non-biological and more angular structure. Moder developed under the homogeneous population of *Picea abies*, while the Amphi makes its way in the more open areas of this same forest with the entry of deciduous trees (*Fagus sylvatica, Acer pseudoplatanus*).

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ijpb14030045/s1, Table S1: Table_Data_PCA (Zampedri 2005).

Author Contributions: Conceptualization, A.Z. and N.B.; methodology, A.Z. and R.Z.; software, R.Z.; validation, R.Z., A.Z., N.B. and J.-F.P.; formal analysis, R.Z. and A.Z.; investigation, R.Z., A.Z.,

N.B., F.V., G.M. and G.Z.; resources, A.Z. and N.B.; data curation, R.Z. and A.Z.; writing—original draft preparation, A.Z.; writing—review and editing, A.Z., N.B., R.G., P.M., C.M., F.V., G.M., G.Z., S.C., A.B. and J.-F.P.; visualization, A.Z., R.Z., N.B. and G.Z.; supervision, A.Z.; project administration, A.Z.; funding acquisition, A.Z., N.B. and R.Z. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: Ethical review and approval were waived for this study. Data were collected and studied in 2002–2005 in accordance with the Declaration of Helsinki. The TESAF (University of Padua) department's current Ethics Committee does not pass judgment on past research.

Informed Consent Statement: Not applicable.

Data Availability Statement: The PCA data are available here: https://we.tl/t-tNktY9ZT0N, accessed on 24 June 2023. For any explanation and additional information, please send a written request to Augusto Zanella (augusto.zanella @unipd.it) or Roberto Zampedri (roberto.zampedri@fmach.it).

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Conflicts of Interest: The authors declare no conflict of interest.

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2.3 HUMUS DYNAMICS AFTER SOIL DISTURBANCES AND IS POTENTIAL ROLE AS AN ECOLOGICAL INDICATOR

Given, as seen before, that the conceptualization and standardization of humus systems is relatively recent, there is currently a lack of scientific research on the effects of windthrow disturbances on forest humus systems.

In one study, Lüscher (2002) examined soils in windthrow-affected areas in Switzerland following the storm Vivian and observed that humus exhibited a shift toward forms characterized by increased biological activity, accelerated organic matter turnover, and enhanced mixing with the mineral fraction. These findings were corroborated by Don et al. (2012), who reported a reduction in organic horizons and a shift toward more decomposed state of organic matter in windthrow-affected areas. Similarly, Salmon (2018) observed comparable dynamics in the humipedon of mechanically cleared forest patches, where the most dominant humus system was Mull, and the organic carbon content was lower than in mature forest stands, characterized by Amphi or Moder Humus systems. These effects were more pronounced in south-facing areas, indicating that temperature plays a key role in humipedon dynamics.

Given the direct interdependence of humus systems to specific ecological factors, a small but growing body of research is beginning to explore the potential use of Humus as an ecological indicator.

For instance, Andreetta et al. (2011) demonstrated strong correlations between humus forms and topsoil carbon stocks in Mediterranean environments. Hellwig et al. (2018) found that humus has significant potential as an indicator of soil chemical and microbiological properties, such as enzymatic activity and the C/N ratio, in high mountain soils. Pintaldi et al. (2018) highlighted correlations between humus forms and soil susceptibility to water erosion, while Moscatelli et al. (2017) identified humus forms as potential dynamic ecological indicators in treeline ecotones.

In order to validate humus as an ecological indicator, however, it is essential to assess its evolution dynamics after disturbances.

The objective of the article, entitled "Evolution of forest humipedon following a severe windstorm in the Italian Alps: a focus on organic horizon dynamics", is to gain insight into the dynamics of humus following a wind disturbance by identifying the factors responsible for the observed changes. The article's primary focus is on the evolution of organic horizons under diverse selected land cover conditions, identified as targeted key microhabitats.

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Evolution of Forest Humipedon Following a Severe Windstorm in the Italian Alps: A Focus on Organic Horizon Dynamics

Francesca Visentin [1], Augusto Zanella [2,*], Sara Remelli [1] 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.); cristina.menta@unipr.it (C.M.)
[2] Department of Land, Environment, Agriculture and Forestry, University of Padua, 35020 Legnaro, Italy
* Correspondence: augusto.zanella@unipd.it

Abstract: This study investigates the effects of the 2018 Vaia windstorm on the evolution of humus profiles in forest soils of the north-eastern Italian Alps five years after the disturbance. The humipedon in five soil conditions was compared: intact forest (IF) and permanent meadow (M) for undisturbed soils, and soil under herbaceous cover (G), under dead wood (W), and bare soil (B) for windthrow-affected areas. No difference in pH and soil organic matter content (SOM) emerged within the same soil horizon between IF and windthrow-affected soils. When compared to IF, however, in G and B, a thinning of all O horizons (OL, OF, and OH) was detected, resulting in SOM loss and an increase in pH in the top 15 cm of the humipedon, conditions approaching the values found in M. Amphi was the most frequently occurring humus system in IF, with a shift towards a Mull system observed in all windthrow-affected soils—a shift more marked in G and B, approaching M conditions, but less marked in W, where the O horizon remained thicker. This study underscores the importance of considering soil heterogeneity and humus dynamics when assessing forest recovery and resilience after a severe disturbance.

Keywords: humus system; humus form; amphi; mull; windthrow; soil organic matter; Vaia storm

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1. Introduction

The influence of anthropogenic climate change on the frequency, intensity, duration, and timing of various natural disturbances has been extensively documented—events including fires, droughts, landslides, species invasions, insect and disease outbreaks, together with storms such as hurricanes, windstorms, and ice storms. Such disturbances have the potential to significantly impact forest ecosystems, affecting their composition, structure, and functionality [1–4]. The increasing frequency of catastrophic storm events is of particular concern, since these result in significant timber loss and structural damage to forest landscapes [5].

The Vaia storm, which struck the north-eastern sector of the Italian Alps in October 2018, was an event of particular significance: exceptionally strong winds (speeds up to 200 km/h) caused extensive windthrow damage, resulting in the loss of approximately 8.3 million m^3 of timber across 4500 acres of forest [6,7]. Despite the destructive nature of such events, severe storms are also a fundamental part of forest dynamics, contributing to forest regeneration and enhanced biodiversity [8,9]. Nevertheless, the extended lifespan of trees precludes their rapid adaptation to abrupt environmental shifts [2]. Consequently, the pace of forest recovery and the question of whether the increased frequency of these disturbances undermines long-term forest resilience need further investigation.

Windthrow events can severely impact topsoil. This is mainly due to tree uprooting, which leads, in turn, to the mixing of soil horizons and local changes in porosity and humidity [10–12]. Other factors to be considered are canopy loss and the subsequent increase in microbial activity due to higher solar energy input, leading to a loss of soil organic carbon

(SOC) and a reduction in C/N ratios in the topsoil [13,14]. Finally, windthrow events can result in the accumulation of potentially high amounts of coarse woody debris (CWD) on the topsoil.

While post-disturbance studies have predominantly focused on tree regeneration dynamics and changes in soil chemical properties, there is limited research specifically addressing changes in humus systems or humus forms following environmental cataclysms. Zanella et al. [15] presented a graph illustrating the integration time of fallen branches and logs into the soil after a storm, relative to humus systems. Estimated biodegradation times for whole trees range from 8 years in Mull humus systems to 56 years in Mor and Tangel systems, with longer durations observed for conifers compared to broadleaves.

Recent studies have investigated the influence of factors such as air temperature and soil moisture on litter biodegradation rates. Bayranvand [16] identified altitude and species composition as primary determinants of humus forms and their chemical characteristics. Para systems (e.g., Rhizoforms and Lignoforms) showed slower decomposition rates compared to Terrestrial systems. Elevations and the associated vegetation types (e.g., subalpine forests vs. alpine grasslands) were shown to influence humus form distribution [17].

Humus forms also vary significantly between poorly drained or waterlogged sites and well-drained areas due to the substantial effect of water on soil processes and morphology [18]. Nikpour et al. [19] demonstrated that dividing a region into altitude ranges significantly improves humus form classification accuracy; as soil moisture increases, typically facilitated by higher organic matter content in surface horizons, humus forms tend to shift toward Moder. Forest canopy composition (pure or mixed) and litterfall characteristics contribute to variations in forest-floor properties (Špulák et al.) [20].

The interplay between climate and bedrock type was shown to strongly influence litter decomposition in temperate forests. Michalet and Liancourt [21] highlighted four key patterns based on studies of Abies alba needle decomposition: (i) a marked decrease in decomposition rates from wet oceanic to dry continental sites on calcareous bedrock; (ii) no change in decomposition rates over time in siliceous sites under increasing drought conditions; (iii) an increase in decomposition rates during wet years in dry continental siliceous sites; and (iv) a stronger dependence of decomposition rates on the physical characteristics of bedrock than on climatic trends.

Organic carbon accrual in soils is primarily constrained by carbon inputs and is strongly modulated by factors such as soil texture, mineralogy, climate, and other site-specific properties [22]. Soil microbial communities also vary with forest stand age [23].

The effects of moisture and temperature on the soil's A horizon are twofold, as noted by Zhang et al. [24]: (i) soil moisture regulates the formation and thickening of the A horizon; and (ii) temperature governs solum development.

In moderate temperature regions, A horizons tend to be thicker, while higher temperatures in southern regions lead to shallower A horizons due to accelerated organic matter decomposition. Conversely, low temperatures restrict vegetation growth and organic matter input, limiting A horizon development.

Particularly intriguing are studies on the relationship between humus system dynamics and the forest's silvogenetic cycle, which may indirectly reflect responses to cataclysmic events, such as large-scale canopy openings. These studies suggest that soils evolve alongside tree age in forests, indicating a combined soil–tree cycle wherein the soil "grows with the tree above it" [25–29] (11–15). The environmental conditions of humus formation, along with the climatic influences on the organisms within the diagnostic horizons of various humus systems, were extensively detailed in three Special Issues of the Applied Soil Ecology journal titled Humusica 1, 2, and 3. In Humusica 1 [30], specific topics are addressed as follows: the seasonal and annual formation of forest horizons is discussed in Article 2 [31]; the key characteristics of each horizon are detailed in Article 4 [32]; the features of each humus system are presented in Article 5 [33]; the challenges of observing phenomena at different scales are analyzed in Article 7 [34]; and the organisms associated with each horizon are described in Article 8 [35].

The canopy openings caused by the Vaia storm, through the felling of trees, have exposed the forest floor to climatic variations—such as increased solar radiation, a rise in the water table, and elevated temperatures due to edge effects—that undoubtedly affect humus systems and forms.

With the intent of better understanding the functioning of soil as an ecosystem [36], it has recently been proposed to subdivide the entire thickness of soil into three subunits, each with distinct functional characteristics: humipedon, copedon, and lithopedon [30]. From the bottom to the top, the lithopedon comprises the rocky mineral horizons (R, C); the copedon comprises the mineral horizons of recent formation (B, E); and the humipedon consists of the organo-mineral and organic horizons, comprising the fresh litter (A, O). The humipedon is the most superficial component of the soil profile, situated in contact with the atmosphere or a water body. It is characterized by the accumulation and/or mixing of dead organic matter with the mineral component. Humipedon is dominated by bioturbation processes driven by soil biota and undergoes monthly variations, whereas the formation and alteration of the entire soil profile under normal conditions occurs over a period of centuries or even millennia.

Although humus is an essential component of forest soils, it has often been overlooked in forest studies. Its value as an ecological indicator, however, is increasingly being recognized in recent research, particularly in the European context, where it has been shown to be a good predictor of soil microbiological and chemical parameters such as SOC stock, enzyme activity, pH, and C:N ratio [37–39]. Humus analysis can, therefore, offer a valuable, cost-effective method for monitoring ecological dynamics in forest soils, also accessible to non-soil experts with appropriate training.

The highly heterogeneous environment resulting from severe storms led to the formation of diverse soil microenvironments [8,40] with the potential to act as different pedogenetic patches [40]. The evolution of microarthropod communities in windthrow sites and their relationship with soil chemical parameters, soil respiration, and humus systems have already been discussed in a previous study [41]. The objective of the present research is to examine this patchiness in greater detail, specifically in terms of humus profiles under different soil covers—an investigation focusing on the same windthrow sites as those in Visentin et al. [41]. In detail, humus dynamics is analyzed, focusing on the evolution of diagnostic horizons, particularly organic ones, expanding classification to the form level, and deepening our understanding of humipedon evolution in a severely disturbed mountain forest ecosystem.

2. Materials and Methods

2.1. Study Sites

This study was carried out in the forests of two different municipalities in the north-eastern Italian Alps that had been severely affected by the Vaia storm in 2018. Investigations took place during the summer of 2023 in San Giovanni di Fassa, located in Val di Fassa (Trentino-Alto Adige region), with a total of 60 samples (18 IF, 18 G, 12 W, 3B, 9M), and Tambre, located in Cansiglio forest (Veneto region), with a total of 27 samples (12 IF, 12 G, 3 W). The coordinates of all sampling points surveyed, as well as their altitudes, can be found in Supplementary Materials (Table S1).

In San Giovanni di Fassa, sampling was carried out at elevations between 1600 and 2000 m a.s.l. In this area, the vegetation is characterized by a managed forest primarily composed of spruce (*Picea abies* (L.) H. Karst.) and larch (*Larix decidua* Mill.), with the understory largely composed of species from the class *Polypodiopsida*, with the occasional presence of acidophilic plants from the genus *Vaccinium*. Meadows are dominated by species typical of alpine grasslands, particularly belonging to the *Poaceae* family, and are primarily used for hay production. The geological substrate mainly consists of dolomite limestone. Forest soils are found on slopes with an inclination ranging from 10% to 45% and are classified as Leptosols, with a high content of rocky debris. Occasionally, Podzol can be found, with an eluvial E horizon lying over a cambic B horizon. In contrast, the soils of permanent meadows are those typical of alpine valleys, formed by the deposition of sediment from adjacent peaks. These are characterized by gentle slopes (maximum 5%) and classified as Umbrisols.

The Cansiglio Forest is located on a karst plateau encircled by rocky peaks in the Italian Prealps. The geological substrate predominantly consists of limestone, and the plateau lies at elevations ranging from 900 to 1200 m above sea level. This topographical configuration induces thermal inversion, whereby cold air becomes trapped on the plateau. Consequently, the plateau supports a managed spruce forest, which transitions into a managed beech forest (*Fagus sylvatica* L.) at higher altitudes. The understory mainly consists of species from the *Polypodiopsida* class. A diverse soil mosaic is present, and Phaeozems and Cambisols are the most common soil types in the study areas.

Based on the Köppen–Geiger classification, both areas have a warm-summer humid continental climate (Dfb). The average annual temperature of San Giovanni di Fassa and Cansiglio is 2.4 °C and 6.1 °C, respectively, while annual precipitation is approx. 1885 mm and 2049 mm, respectively.

2.2. Experimental Design

Samplings took place in July 2023. In the two sampling areas, 20 sites were identified (12 in Val di Fassa and 8 in Cansiglio), half of which were located in windthrow-affected areas (Figure 1a,b).

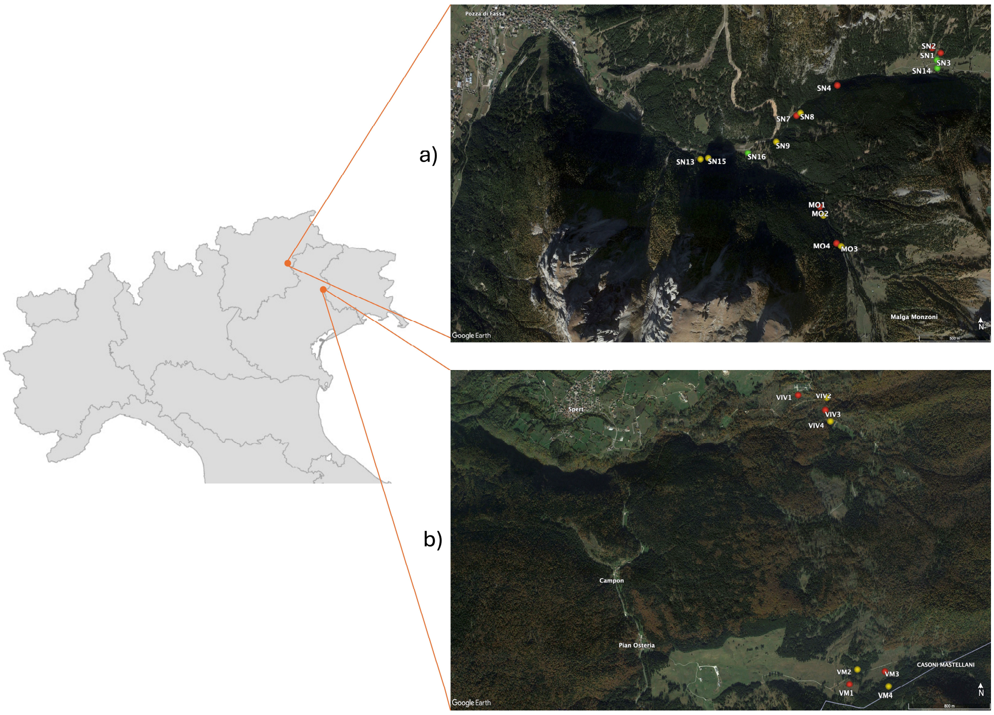


Figure 1. Location of sampling sites in (**a**) Val di Fassa and (**b**) Cansiglio. Yellow dots: intact forest; Red dots: windthrow-affected areas; Green dots: meadows. Figure from Visentin et al. [19].

Regarding windthrow-affected sites, in each site three soil coverage conditions were identified and then, when found, evaluated: patches with herbaceous vegetation cover (grass, G); patches with decaying wood on the soil (W); and patches with bare soil (B). It is important to highlight that these conditions were not uniformly present across all the selected sites. The data collected from these areas were compared with those obtained from undisturbed sites. In particular, one main undisturbed soil coverage condition was identified, i.e., intact forest (IF) adjacent to windthrow areas. In Val di Fassa, a permanent meadow condition (M) was also evaluated with 3 additional sites (Figure 1a) to test the hypothesis that humus type and soil chemical properties of G sites are shifting towards those of adjacent permanent meadows. For each condition present in all sampling sites, 3 replicate subsites were identified, at least 10 m from each other to avoid spatial autocorrelation. A total of 87 replicates were therefore sampled: 60 from Val di Fassa and 27 from Cansiglio. The number of samples for each soil coverage condition was 18 IF, 18 G, 12 W, 3 B, and 9 M for Val di Fassa, and 12 IF, 12 G, and 3 W for Cansiglio.

For each soil coverage condition, the following parameters were analyzed: (1) soil chemical features (pH, soil organic matter content); (2) humus characterization; (3) soil respiration; and (4) soil microarthropods. The classification system used to name the studied soils is the World Reference Base for Soil Resources (WRB) of the International Union of Soil Sciences. This paper focuses on humus systems and forms and how they have evolved five years after disturbance. For results on soil microarthropod communities and their relationship with soil chemical properties, soil respiration, and humus systems (see Visentin et al.) [41].

2.3. Humus Classification and Chemical Analysis

For each subsite, a soil profile was opened to classify humus forms following the methodology described by Zanella et al. [42]. After the maximum depth of the A horizon was reached, the following data were collected: thickness of all diagnostic horizons found in each profile (OL, OF, OH, A); qualitative characteristics of aggregates composing the A horizon (whether biomacro- (maA), biomeso- (meA), or biomicrostructured (miA), massive (msA), or single grained (sgA)); sharpness of the transition between O and A horizons. When occurring, para horizons (Ligno, Rhizo, or Bryo) were noted and measured. Based on these data, the humus system and form of each replicate site were classified. As some humipedon profiles, mainly in windthrow-affected areas, were disturbed and horizons not always easily discernible, the following criteria were applied: (i) when the horizon was discontinuous or <3 mm, the assigned thickness was set equal to 0; (ii) if disturbed or mixed with other horizons, the minimum undisturbed thickness of a horizon was recorded; (iii) para horizons were assigned to the O or A horizon according to the amount of organic matter present (generally “Rhizo” horizons were assigned to the A horizon, whereas “Ligno” and “Bryo” to the O horizon).

After registering the thickness of O (OL + OF + OH) and A horizons, a cylindrical soil core (approximately 100 cm^3) was collected from each horizon for chemical analysis. In the laboratory, each soil core was homogenized and sieved to 2 mm. The pH was determined using a pH meter (Xylem Analytics, Weilheim in Oberbayern, Germany) in a soil-distilled water solution with a 1:5 volume ratio [43]. SOM was assessed via loss-on-ignition, wherein 6 g of pre-dried soil (at 105 °C) was placed in a muffle furnace (Nabertherm GmbH, Lilienthal, Germany) at 160 °C for 6 h, followed by 400 °C for 4 h [44]. SOM was subsequently calculated using the following formula:

$$\text{SOM\%} = [(\text{Weight}_{160\,^\circ\text{C}} - \text{Weight}_{400\,^\circ\text{C}})/\text{Weight}_{105\,^\circ\text{C}}] * 100$$

2.4. Statistical Analysis

All statistical analyses were performed with R software v 4.2.3.

Non-parametric tests were applied after ANOVA assumptions were tested (package: stats) and not met. The Kruskal–Wallis test followed by the Mann–Whitney test with Holm correction (package: stats) was used in order to assess the differences between conditions of the following variables: pH, SOM, thickness of O horizons, and maximum depth of O horizon. Initially, the analysis was conducted separately for the two areas. However, since both areas exhibited similar variation trends, the analysis was repeated using combined data from both areas.

Subsequently, for each replicate, a single value was determined for each soil chemical parameter (pH and SOM) representing the mean for the O and A horizons within the first 15 cm of the humipedon. This value was calculated as a weighted mean, taking into account the relative thicknesses of the O (OL + OF + OH) and A horizons within the top

15 cm of the humipedon. Finally, Kruskal–Wallis and Wilcoxon tests were performed on these new variables.

3. Results

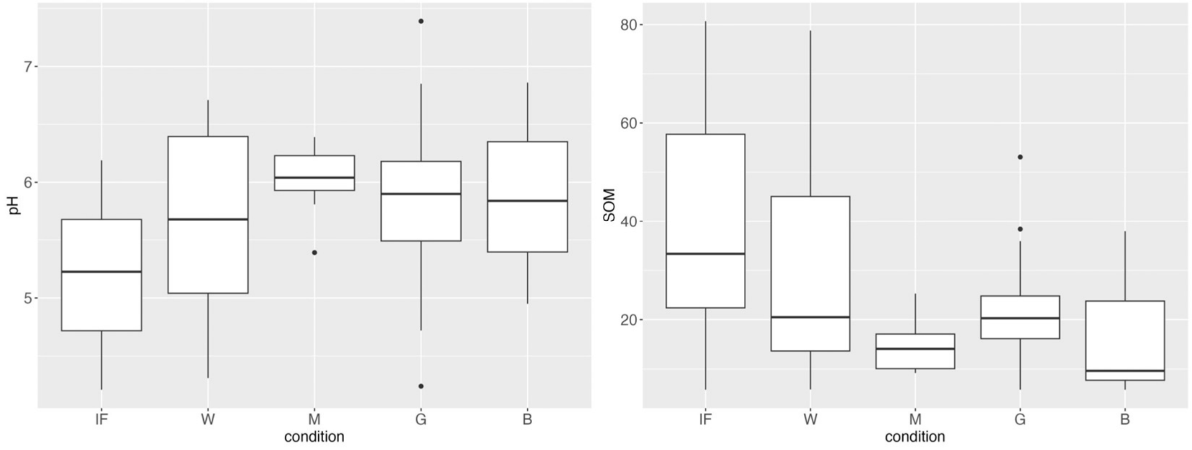
3.1. Soil Chemical Features

Soil organic matter content and pH in O and A horizons (Table 1) did not differ statistically between conditions ($p > 0.05$).

Table 1. Means and standard errors of pH and soil organic matter content (SOM) of O and A horizons in each soil coverage condition. 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.

Condition	pHO Mean ± SE	pHA Mean ± SE	SOM O% Mean ± SE	SOM A% Mean ± SE
IF	5.01 ± 0.1	5.48 ± 0.16	56.23 ± 3.61	21.72 ± 2.08
M	5.8 ± 0.09	6.03 ± 0.1	42.63 ± 1.87	13.89 ± 1.22
G	5.39 ± 0.1	5.95 ± 0.13	43.92 ± 2.99	16.76 ± 1.07
W	5.19 ± 0.27	5.93 ± 0.22	57.98 ± 7.04	18.8 ± 3.09
B	-	5.88 ± 0.55	-	17.78 ± 10.13

In contrast, when the weighted mean of SOM and pH values of the first 15 cm of the humipedon was considered, a trend of decreasing SOM and increasing pH in G and B conditions (but not in W) in windthrow sites compared to IF emerged ($p < 0.01$ for all comparisons), with G values approaching those of M, as reported in Visentin et al. [19] (Figure 2).

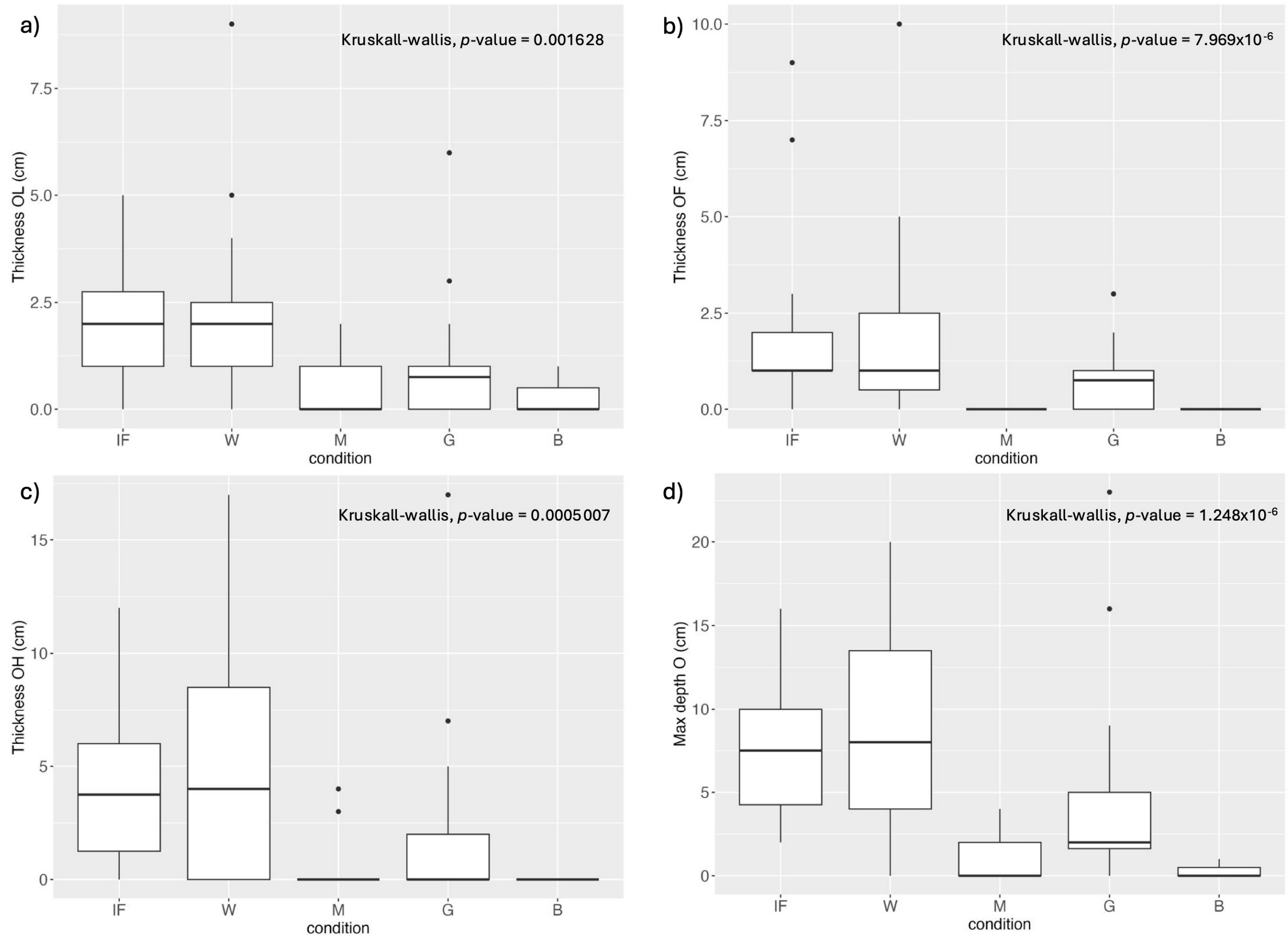


(**a**) (**b**)

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

3.2. Diagnostic Horizons

In undisturbed soils, all O diagnostic horizons were thicker in IF than in M. In windthrow-affected areas, OL, OF, and OH were thinner in G and B than in undisturbed forest, while the thickness of such horizons in W did not significantly differ from IF ($p > 0.05$). The same trend was observed when the maximum depth reached by the complete O horizon was examined (Figure 3).



	IF-W	IF-M	IF-G	IF-B	M-G	M-B	M-W	G-W	G-B	W-B
a)		*	*				*			
b)		***	**	*	*		**	*		
c)		**	**	*						
d)		***	***	*	*		**	*	*	*

Figure 3. Boxplot representing the thickness of (**a**) OL; (**b**) OF; (**c**) OH horizons; and (**d**) maximum measured depth of the entire O horizon (OL + OF + OH) in each soil coverage condition. IF = intact forest; W = under decaying wood in windthrow areas; M = permanent meadow; G = under grass in windthrow areas; B = bare soil in windthrow areas. For each boxplot, the significance of the Kruskal–Wallis test is provided. In the table, the significant couples are reported: * = $p < 0.05$, ** = $p < 0.01$, *** $p < 0.001$.

3.3. Humus Classification

Regarding undisturbed soils (Table 2 and Figure 4), Amphi humus systems accounted for 90% of the observations in IF, with only two observations of a Moder system and one of a Mull. Eleven different humus forms were observed, with the most frequent being 14 observations of Pachyamphi (Figure 5a). Para forms were also frequently present: Rhizo, Ligno, but mostly Bryo, due to the important presence of mosses in undisturbed forest soils. In permanent meadows, the Mull humus system accounted for two-thirds of the observations, with Amphi accounting for the remaining systems, all of which belonged to just one site—a permanent meadow occasionally pastured by livestock. In 83% of the cases, the Mull humus form was Eumull, with Rhizomull observed in only one case.

Table 2. Humus systems and forms, and their relative frequency, observed in the two study areas. 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.

Condition	Humus System	Number of Observations	Humus Form	Number of Observations	%
IF	Mull	1	Dysmull	1	100
	Moder	2	Dysmoder	1	50
			Ligno Dysmoder	1	50
	Amphi	27	Pachyamphi	6	22.22
			Bryo Pachyamphi	6	22.22
			Rhizo Pachyamphi	1	3.7
			Ligno Pachiamphi	1	3.7
			Leptoamphi	3	11.11
			Eumesoamphi	3	11.11
			Bryo Eumesoamphi	6	22.22
			Eumacroamphi	1	3.7
M	Mull	6	Eumull	5	83.33
			Rhizo Mull	1	16.67
	Amphi	3	Pachyamphi	2	66.67
			Leptoamphi	1	33.33
G	Mull	14	Rhizo Mull	5	35.71
			Eumull	4	28.57
			Dysmull	4	28.57
			Ligno Rhizo Mull	1	7.14
	Amphi	16	Leptoamphi	5	31.25
			Pachyamphi	2	12.5
			Rhizo Pachyamphi	2	12.5
			Eumesoamphi	2	12.5
			Rhizo Eumesoamphi	4	25
			Bryo Eumesoamphi	1	6.25
W	Mull	7	Rhizo Mull	3	42.86
			Rhizo Ligno Mull	1	14.28
			Eumull	1	14.28
			Mesomull	1	14.29
			Dysmull	1	14.29
	Amphi	6	Leptoamphi	1	16.67
			Ligno Leptoamphi	1	16.67
			Pachyamphi	2	33.33
			Ligno Pachyamphi	1	16.67
			Rhizo Eumesoamphi	1	16.67
	Tangel	2	Eutangel	1	50
			Ligno Leptotangel	1	50
B	Mull	2	Eumull	2	100
	Amphi	1	Leptoamphi	1	100

In windthrow-affected areas (Table 2 and Figure 4), a marked tendency towards a Mull humus system was observed compared to IF (Figure 5d). Mull accounted for almost 47% of the observations in G and W, whereas it accounted for two-thirds of the observations in B. Various Mull forms were observed in G, with Rhizo being the most frequent para form (Figure 5b). One Ligno para form was detected, probably left over from the previous undisturbed forest. In G, the Amphi humus system covered the remaining observations. Leptoamphi and Eumacroaphi were the most frequent forms—a result in line with the thinning of the O horizon under this soil coverage condition. In W, on the other hand, alongside the Mull and Amphi humus systems, the Tangel system accounted for 13% of the observations and was found only under this soil coverage condition. The Rhizo paraform was observed when the soil coverage was composed of a single log surrounded by herbaceous vegetation. The presence of Ligno could mainly be attributed to the presence of an OL or OF Ligno horizon (Figure 5c). Finally, only Mull and Amphi were recorded in B.

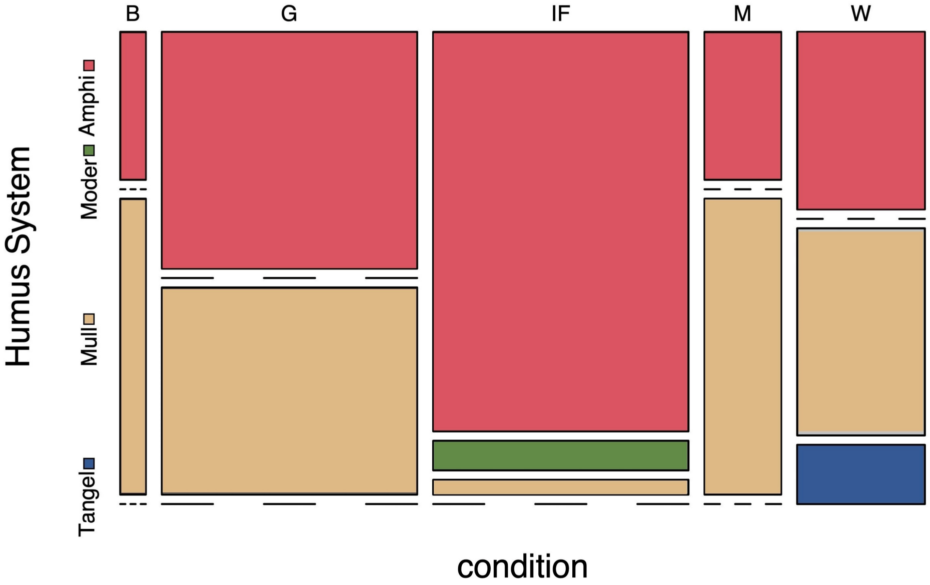


Figure 4. Mosaic plot comparing the distribution of the humus systems across the investigated soil coverage conditions: B = bare soil in windthrow areas; G = under grass in windthrow areas; IF = intact forest; M = permanent meadow; W = under decaying wood in windthrow areas.

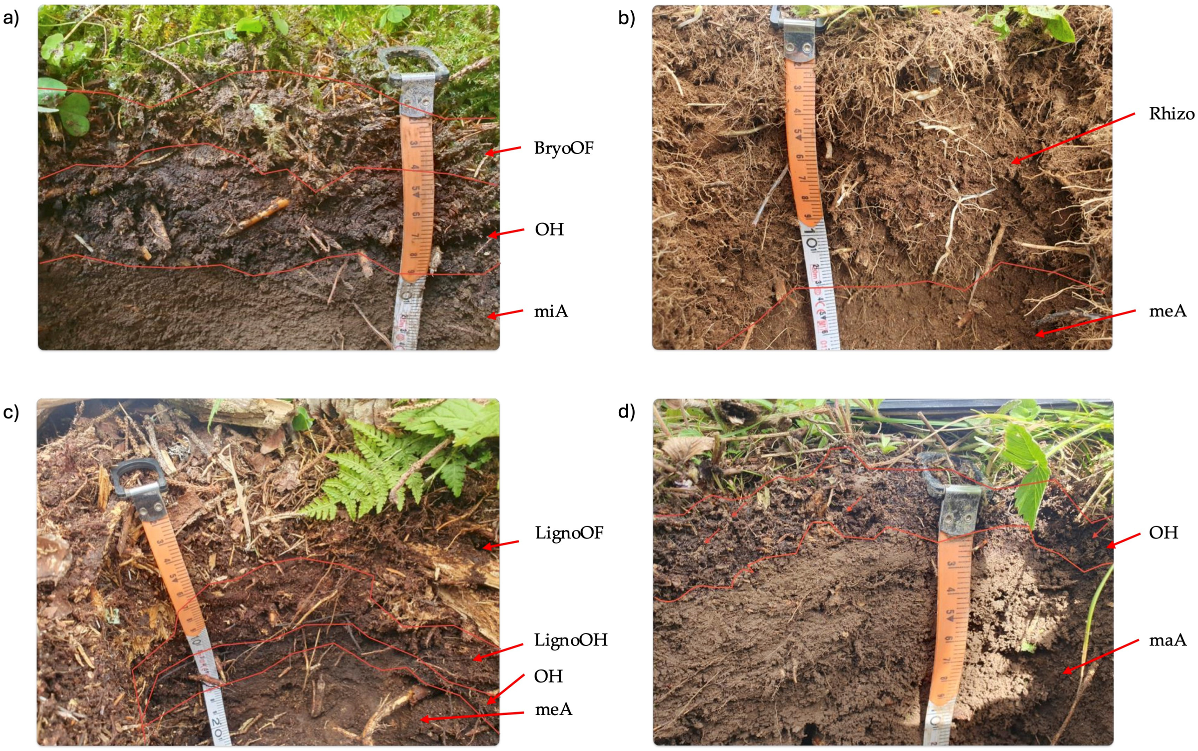


Figure 5. Examples of humus profiles from the selected study sites; red lines demarcate the diagnostic horizons: (**a**) Cansiglio, IF: Bryoeumesoamphi; (**b**) Val di Fassa, G: Rhizomull; (**c**) Val di Fassa, W: Lignoleptotangel; (**d**) Cansiglio, G: Eumesoamphi evolving towards a Mull system. Here, the O-A transition is very irregular; red arrows indicate the organo-mineral casts in the thickness of OH.

4. Discussion

This study aimed to evaluate humus dynamics, with particular attention to the evolution of the diagnostic horizons in several soil coverage conditions five years after the severe Vaia windstorm, which occurred in 2018.

Our results evidenced no significant variation either in soil organic matter (SOM) content or pH when conditions within the same horizon were compared. However, when the mean value of the top 15 cm of the humipedon—the layer in which most soil fauna typically resides, playing a crucial role in soil health and nutrient cycling—was taken as a reference, a discernible difference emerged between soil coverage conditions. This difference can be accounted for by the thinning of all O diagnostic horizons (OL, OF, and OH) in soils under herbaceous cover (G) and in bare soils (B) in windthrow-affected areas when compared with intact forest (IF). This result is in line with a study by Don et al. [45], where the soil organic carbon (SOC) stock in the Tatra mountains 3.5 years post windthrow disturbance was investigated. This study revealed a decrease in SOC stock in litter horizons in cleared areas but no similar decrease in non-cleared areas that had been left to natural regeneration; no variance in SOC stock was found in organo-mineral and mineral horizons. As demonstrated in other studies [46,47], topsoil SOC turnover rate is driven by temperature, increasing along with soil depth. Consequently, in organic (O) horizons, the mean SOM residence time is significantly shorter than in organo-mineral (A) horizons, which are more protected from solar radiation. This results in the formation of different SOM "stability pools", with the topsoil layer potentially exhibiting greater activity than deeper layers [48]. In line with these studies and with the findings of Kobler et al. [49] and Mayer et al. [50], our data suggest that in windthrow-affected areas with no soil coverage, canopy loss and the subsequent increase in solar energy may have enhanced the mineralization of the organic matter in the OL, OF, and OH horizons, which represents the less stable pool. This may have resulted in (i) the thinning of the organic horizons and the shift from an Amphi to a Mull system, and (ii) the net loss of SOM and a pH increase in the top 15 cm of the humipedon. Following this, the humipedon conditions of G and B approached those of mountain permanent meadows. A similar shift toward a Mull system was also observed following clear cuts in mature stands [51] and under mature and dying spruce trees, which, within the forest sylvogenetic cycle, favored forest regeneration [26,27,52].

On the other hand, in soils covered by dead wood (W), the changes were less pronounced than those observed in G and B. The turnover of SOM in W was slower due to the physical protection of timber, although our study revealed considerable variability. It is noteworthy that the only two observations of Tangel systems were found in the W plots. This humus system is typical of upper mountain climate with rigid ecological conditions and is characterized by slow organic matter turnover [33].

Humus forms registered in intact forest were in line with those expected in carbonate-rich alpine soil [31] and with those found in a survey of Ponge et al. [53] in forests in the Veneto region.

In windthrow-affected sites, the characterization of soil horizons was often challenging due to their irregularity and mixing. Disturbances in some OH horizons were observed, often marked by the mixing activity of earthworms, which was evidenced by organo-mineral droppings within the OH horizon and an irregular transition between the OH and A horizons. This bioturbation is expected to eventually result in the complete disappearance of the OH horizon—a process described by Zampedri et al. [28] for bipolar Amphi systems, though in our study the shift is not being driven by stand aging but by the disruption of the forest ecosystem caused by the storm. These evolving humipedons were classified as Amphi systems due to the current presence of the OH horizon, but the ongoing trend toward Mull formation was clearly evident.

Concerning Para humus forms, the most interesting were found to be the Ligno forms (Figure 5c). In IF, the registered Ligno horizons were OH horizons: residues of wood decomposition, incorporated in the humipedon profile and broken down by soil animals and microflora until it approached the amorphous state typical of OH. Tatti et al. [54] classified this advanced stage of decomposition—corresponding to the fifth stage in Maser et al. [55]—as the third stage of the decomposition process, or the "integration stage" in the soil. It is estimated that dead wood of *Picea* spp. takes from 61 to 286 years to reach this complete stage of decomposition, depending on temperature, moisture, C concentration, contact with the forest floor, and the composition of the decomposer community [56,57]. In W, on the other hand, we found dead wood in decomposition stage 1 or 2, which was mainly incorporated in the OL or OF horizons (rarely in the OH horizon) or found in the form of logs and stumps. Studies by Błonska [58,59] indicate that the maximum transfer of organic carbon into the soil occurs at the fifth stage of decomposition. This suggests that unless dead wood from the Vaia storm is left in place for several decades, it will not significantly contribute to the accumulation of soil organic carbon in these profiles. Leaving dead wood provides the additional benefit of enhancing forest regeneration, as demonstrated by Bernier et Trosset [60], who found that the growth rate of spruce and larch was higher in humus form integrated with rotten wood (third stage of decomposition, [36]) rather than in humus that did not contain any dead wood.

5. Conclusions

The question of whether soils will act as a sink or source of atmospheric carbon under climate change remains a topic of ongoing debate, highlighting the urgent need for comprehensive surveys of the relationships between humus systems and carbon storage in a wide range of both undisturbed and disturbed ecosystems. Collecting reliable data on humus systems and their carbon stock dynamics is crucial for improving global predictive models and making informed decisions about sustainable land management practices in the face of climate change.

Our study suggests that the passage of a severe storm, such as the Vaia storm, significantly increases the heterogeneity of the affected forest floor. Despite evolution dynamics still being underway, we observed a relatively rapid response to the disturbance on the part of the humipedon. The formation of Mull patches and the presence of Lignoforms are likely to promote forest regeneration. However, a critical concern emerging from our study is the loss of soil organic matter, which could have significant long-term effects on soil fertility and carbon storage. To mitigate this, we recommend leaving a portion of dead wood on-site to undergo natural decomposition, which could help preserve soil organic matter levels and enhance the resilience of forest ecosystems.

Ultimately, our study underscores the importance of understanding how disturbance events, such as severe storms, interact with humus systems and soil organic matter in forest ecosystems. Collecting detailed data on these dynamics is essential for refining global climate models and informing land management decisions. Future research should prioritize long-term monitoring of these events across diverse ecosystems to improve our ability to predict and manage the effects of climate change on soil health and forest regeneration.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15122176/s1, Table S1: The coordinates (lat, long) of all sampling points surveyed, as well as their altitudes (msl).

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3. MICROARTHROPODS DYNAMICS FOLLOWING A WIND DISTURBANCE

3.1 MICROARTHROPODS AS BIOINDICATORS

In the aftermath of catastrophic disturbances, such as extreme storm events, assessing forest damage is crucial for understanding ecosystem responses and planning for future management. Monitoring forest regeneration and evaluating forest management practices through appropriate indicators is key to ensuring effective post-disturbance recovery. In recent decades, increasing attention has been directed toward the importance of biological indicators in evaluating soil health. UNESCO Biodiversity Indicator Partnership (2006) stated that "The principle behind the indicator concept is that the characteristics of an easily measured feature convey information about more than itself, summarizing and communicating complex information in a way that can be quickly understood"

This is particularly relevant for biological indicators, which utilize biota to assess the impacts of habitat alterations over time, basing on the idea that populations evolve adaptive strategies to maximize growth and reproduction within specific environmental ranges. When environmental conditions fall outside these optimal ranges, an organism's physiology or behavior may be negatively impacted, leading to reduced fitness. This, in turn, can disrupt population dynamics and alter community structure (Holt & Miller, 2010). Therefore, indicator taxa or groups can be selected based on the identification of predictive relationships between indicators and environmental variables, and, most importantly, the development and testing of hypotheses based on the observed correlative patterns (McGeoch, 1998). Studying the dynamics of these selected indicators organisms under different stressors is essential not only for understanding how ecosystems respond to environmental changes, but also to validate the utilization of that species or group as an indicator.

Among soil fauna, microarthropods, especially in forest soils with well-developed litter and humus layers, are notable for their high species diversity. These invertebrates exhibit complex relationships with their ecological niches and their life cycles span areas representative of the site under investigation making them valuable for bioindication purposes. Several species within this group have already been identified as useful biological indicators of soil quality, but, most importantly, the stability of community composition at a given site offers a strong basis for assessing changes in soil properties and the effects of both natural disturbances and human activities (Parisi, 2001; Van Straalen, 1998). Specifically, microarthropods that were extensively studied as indicators are Collembola and Acarina, but other parameters are used as reliable indicators of soil health and quality, like their abundance, feeding activity, and their degree of adaptation to the soil environment. (Gruss et al., 2022).

3.2 MICROARTHROPOD COMMUNITY DYNAMICS AFTER A WIND DISTURBANCE

It is largely known that microarthropods plays a crucial role in litter degradation and soil aggregates formation. Their feeding habits range from litter transformers and primary decomposers to saprotrophs, microbial grazers, and predators of other soil fauna, influencing the formation of soil organic matter at all levels of the soil food web (Nielsen et al., 2015). Among their most important functions, microarthropods transform fresh organic matter, redistribute organic matter and microbes within the soil matrix, create hotspots of microbial activity, play an important role in soil aggregation, and contribute to the release of nitrogen and phosphorus during litter decomposition (Carrillo et al., 2011; Maaß et al., 2015; Soong & Nielsen, 2016). These activities, considering their ubiquitous presence in soil ecosystems, make microarthropods key actors in the dynamics of the Humipedon.
Despite their importance, notions about the details of how they contribute to soil and humus formation are still scarse and the dynamic relationships between microarthropod communities and humus formation in disturbed environment are still largely unknown.

Several studies have explored the effect of forest disturbances on arthropods, generally reporting an overall increase in total biodiversity following a disturbance (Duelli et al., 2002, Wermelinger et al, 2003) but the effects on forest ecosystems differ greatly with disturbance severity and time since disturbance (Thom and Seidl, 2016). Among disturbances, the consequences of fire and severe drought on arthropods are the most studied. In temperate and boreal forests fire determine a strong decrease of abundances and diversity of soil arthropods (Gongalsky and Persson, 2012; Lóšková et al., 2013; Wehner et al., 2021). Malmström et al. (2008) found that the decrease of abundances was related to fire intensity and that fire affected for years the abundances of Oribatida and Protura but other taxa like Collembola and Mesostigmata begin to recover as sast as few months after the disturbance. In Mediterranean forests, though, the decrease in abundance is not so marked and depend strongly on vegetation cover, with pinewood being the most unfavorable forest for microarthropods (Santorufo et al., 2024; Mantoni et al., 2020) Regarding wind disturbances, fewer studies have specifically addressed the impact of windthrow on soil microarthropod communities and the studies were conducted exclusively in Europe and in temperate or boreal forests, the most prone to winthrows. The findings from existing research often conflict with one another or are not directly comparable, primarily due to three key issues: i) most studies focus on epigeic arthropods, or, when endogeic arthropods are considered, attention is typically only given to the most abundant and well-studied taxa, such as Acarina and Collembola (Wermelinger et al., 2003; Bouget & Duelli, 2004; Perry & Herms, 2019) (ii) many studies examine microarthropod communities at a specific time post-windthrow, without accounting for their temporal evolution. The few studies that do investigate long-term dynamics suggest that recovery is slow, continuing even a decade after the disturbance (Duelli et al., 2002; Sterzyńska & Skłodowski, 2018) (iii) while many studies assess the effects of different management intensities at windthrow sites, few account for the soil heterogeneity created by the disturbance, potentially overlooking micro-scale dynamics that become evident only at the micro-site level (Bouget & Duelli, 2004; Coyle et al., 2017; Hirao et al., 2008).

Consequently, our current understanding of the overall impact of windthrow on the entire microarthropod community remains limited, making it challenging to determine which post-windthrow management practices are most effective in maintaining the resilience of these communities. What is clear, however, is that microarthropods exhibit varied responses to windthrow disturbances.

With regard to the overall microarthropod community, two studies conducted one year after separate windthrow disturbances in Europe (Menta et al., 2022; Urbanovičová et al., 2010) found no significant differences in the abundance and number of microarthropod groups between intact forest and windthrow sites. However, Urbanovičová (2010) reported a decrease in diversity indices in damaged areas, indicating a dominance of Collembola in the microarthropod community, while Menta et al. (2022) found no clear trend in Collembola populations.

Specifically, Collembola, the most studied taxa, are seen to exhibit differing responses between epigeic and ipogeic species. For exemple Farská et al. (2014) observed that species with a well-developed furca increased in response with increased post-windthrow management. Although they found no significant differences in diversity indices across different management intensities, a notable shift in species composition and functional groups was observed. Sterzyńskaa and Skłodowski (Sterzyńska & Skłodowski, 2018) observed that collembolan community composition recovery is slow and varies between natural pine regeneration and regeneration by planting, with Collembola communities displaying differing sensitivity to environmental changes caused by varying degrees of canopy opening due to windthrow. Cuchta et al. (2012) reported higher densities of Collembola in non-extracted windthrow stands compared to intact forest and found the lowest densities in clear-cut stands. Conversely, Urbanovičová et al. (2010) found that the community was dominated by Collembola in damaged sites, where their activity was significantly higher, and species composition shifted towards a dominance by species characteristic of open habitats. In summary, while data on abundance and diversity are not always consistent, the increase in light irradiation in windthrow sites appears to drive diversification in Collembola community structure, favoring species characteristic of open habitats.

Oribatid mites appear to be particularly sensitive to cumulative disturbances, Wehner et al. (2021) observed that abundance and species richness decreased up to 87% following combined drought and windthrow events, with the reduction being more pronounced in bare soil. In accordance with this study, Kreibich et al. (2010) observed a decline in Oribatid mite abundance immediately after a storm and a subsequent slow increase after a four-year period.

Similar to Collembola, Farská et al. (2013) reported a significant shift in the Oribatida community from fungivory and carnivory to detritivory as management intensity increased. Hirao et al. (2008) similarly noted an increase in epigeic herbivorous insects in windthrow-affected sites.

As for the lesser-studied groups, the only study focused exclusively on Protura found that disturbances negatively impacted proturan diversity and abundance, with the greatest effects observed under multiple disturbances. However, differences in edaphic factors were a stronger driver of variability in the distribution and abundance of Protura than the disturbances themselves, suggesting that soil biogeochemistry and resource availability exert greater influence on proturan assemblages than forest disturbances (Sterzyńska et al., 2020). In contrast, Menta et al. (2022) found no clear trend in proturan assemblages after windthrow but reported a significant reduction in the presence of insect larvae (mainly Diptera) in damaged areas.

In this context, this research phase focused on studying the evolution of the microarthropod community in the areas affected by the windthrow, taking into account the heterogeneity created by the windthrow itself. This was done at the same sites previously identified in the two sampling areas. In order to evaluate the impact of the wind disturbance on the overall health of the microarthropod community, it was decided that the specimens extracted from each soil samples should be classified at the class level for Myriapoda and the order level for Hexapoda, Chelicerata and Crustacea. In the case of mites, two groups were considered: Oribatida and Acarina. This was due to 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, given that they occupy different ecological niches compared with their adult forms.

The QBS-ar index was applied as a tool to assess soil biological quality, as it has been shown to be sensitive to soil degradation following disturbances (Mantoni et al., 2020; Menta et al., 2018). Additionally, it was used to evaluate whether certain microarthropod communities could be linked to varying levels of soil biological quality.

Once the communities in the different microhabitats had been characterized, an investigation was undertaken into the relationships between the structure of microarthropod communities, the humus forms and soil organic matter dynamics.

This second research phase led to the publication of one research paper presented below:

1) Visentin, F.; Remelli, S.; Zanella, A.; Menta, C. Windthrow Impact on Alpine Forest Humipedon: Soil Microarthropod Communities and Humus Dynamics Five Years after an Extreme Windstorm Event. *Land* **2024**, *13*, 1458. https://doi.org/10.3390/land13091458

   Specific aim: To examine the characteristics of the microarthropod community as a whole, across the same soil cover conditions previously identified, investigating their functional relationships with humus systems, soil chemical properties, and soil respiration.

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Article

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.

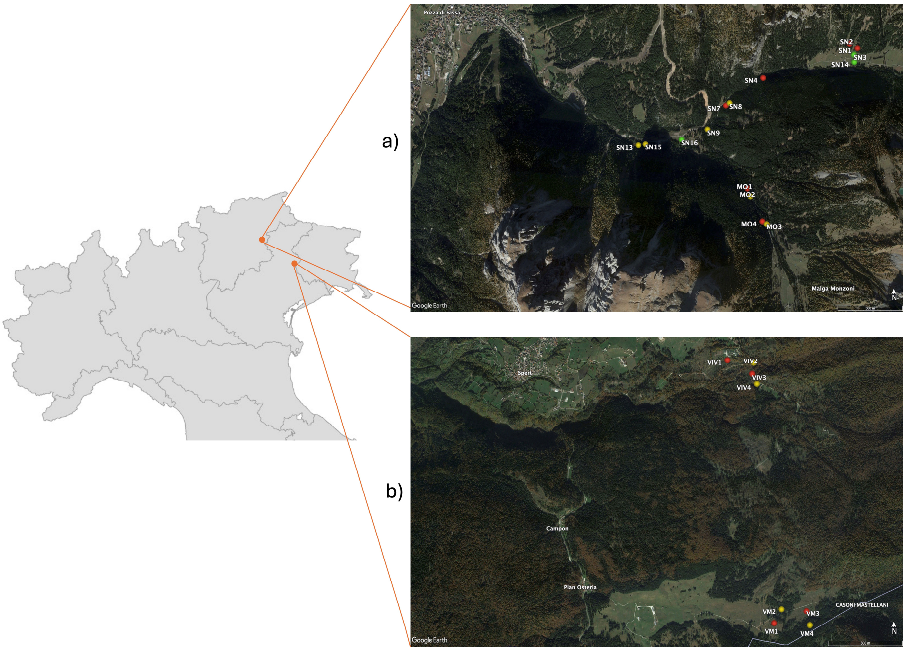

Figure 1. Location of sampling sites in the (**a**) Val di Fassa and (**b**) Cansiglio areas. Yellow dots: intact forest; red dots: windthrow areas; green dots: meadows.

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:

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

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 ± 21.38%), which was higher than in both G and M (Figure 2b).

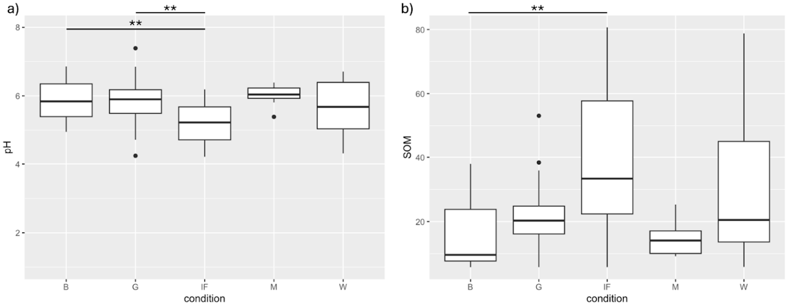

Figure 2. Boxplot of the (**a**) pH and (**b**) soil organic matter (SOM; %) in the topsoil (15 cm) of each soil coverage condition in both sampling areas. B = bare soil in windthrow areas; G = under grass in windthrow areas; IF = intact forest; M = permanent meadow; W = under decaying wood in windthrow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

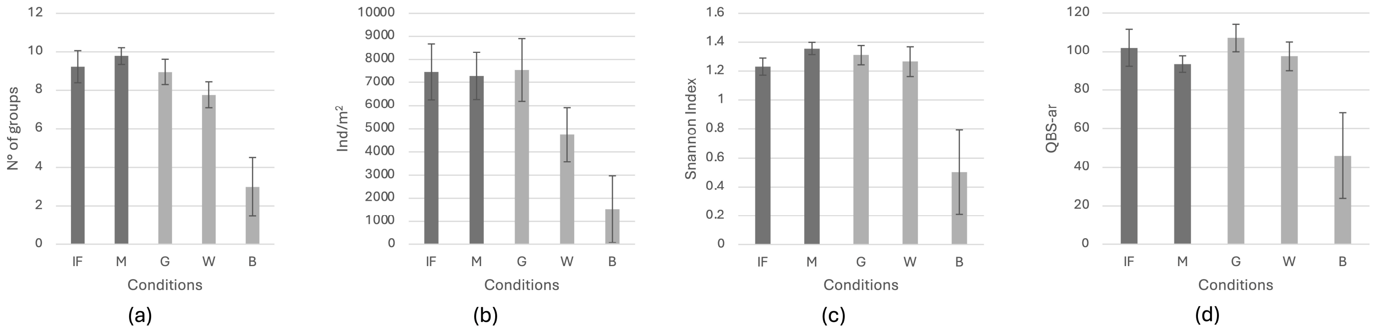

Figure 3. Histograms representing the mean and standard error of the (**a**) number of microarthropod groups, (**b**) number of specimens per square meter (total abundance), (**c**) Shannon diversity index, and (**d**) QBS-ar index for each soil coverage condition in Val di Fassa. IF = intact forest;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

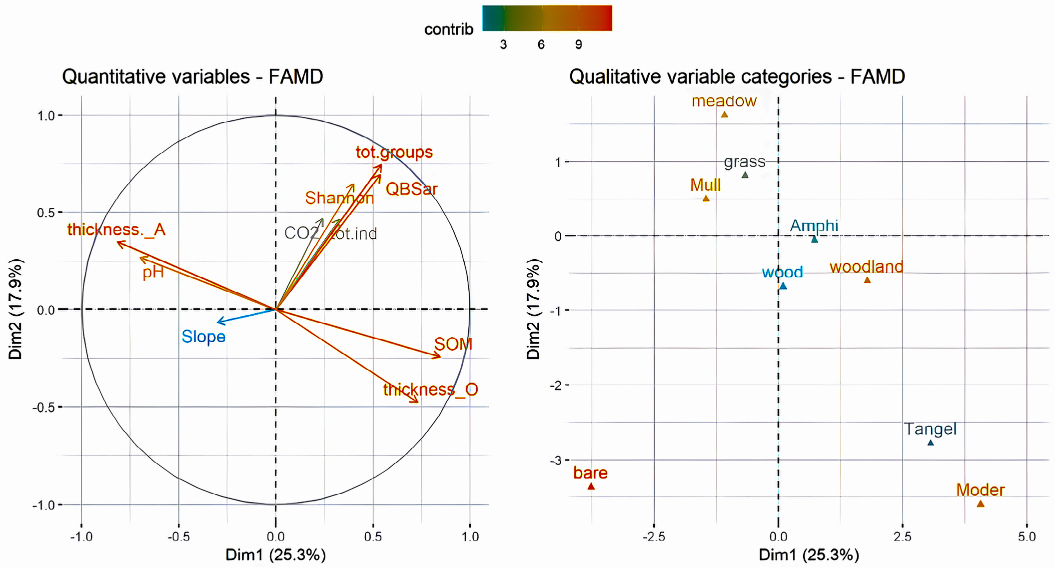

Figure 4. FAMD graph representing all the quantitative and qualitative variables from the Val di Fassa area.

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

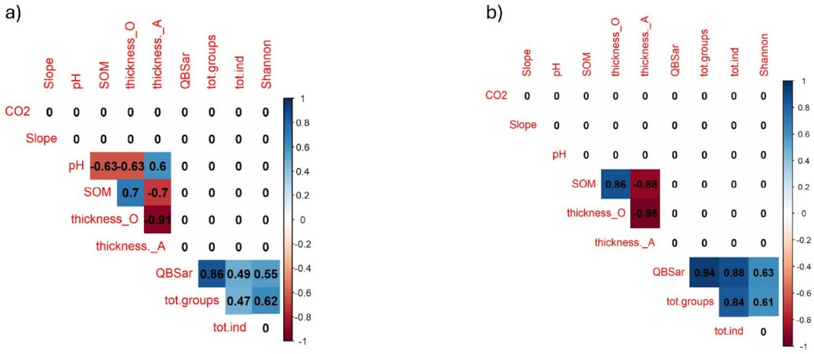

Figure 5. Spearman correlation output between the quantitative parameters in (**a**) Val di Fassa and (**b**) Cansiglio. Numbers indicate the positive or negative correlation coefficient.

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).

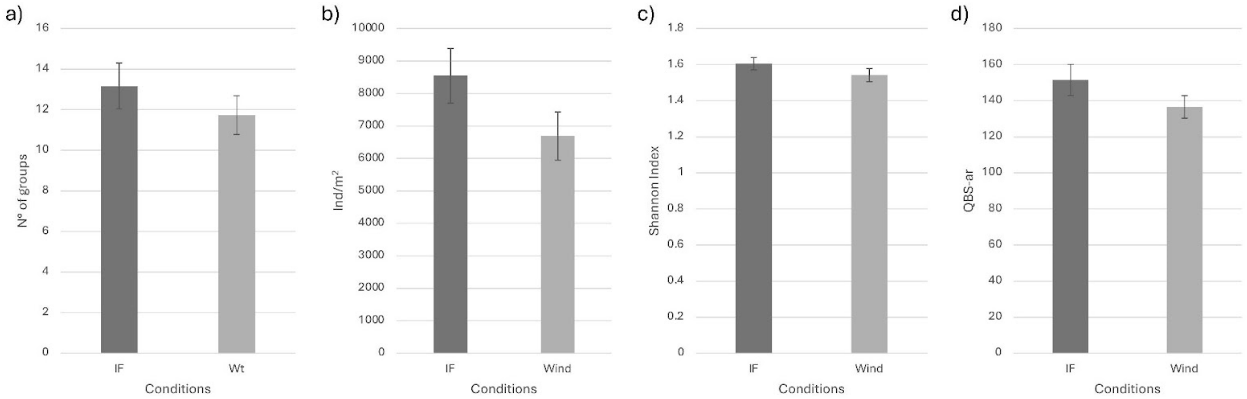

Figure 6. Histograms representing the mean and standard error of the (**a**) number of microarthropod groups; (**b**) number of specimens per square meter; (**c**) Shannon diversity index; and (**d**) QBS-ar index for each soil coverage condition in Cansiglio. IF = intact forest; Wt = windthrow area.

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.

Author Contributions: Conceptualization, F.V., C.M., S.R. and A.Z.; Methodology, F.V. and C.M.; Investigation, F.V. and S.R; Data curation, F.V.; Formal analysis, S.R.; Writing—original draft preparation, F.V. and S.R.; Writing—review and editing, C.M. and A.Z.; Supervision, C.M. and A.Z.; Funding acquisition, C.M. All authors have read and agreed to the published version of the manuscript.

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4. CONCLUSIONS

Five specific objectives were set for this research work:

(i) To characterize the various microhabitats resulting from windthrow damage in two Italian Alpine forests in terms of soil coverage and chemical soil parameters.

(ii) To study the evolution of humus profiles within these microhabitats and assess whether they correlate with soil coverage conditions.

(iii) To characterize the microarthropod communities within the same microhabitats and determine whether a discernible link exists between microarthropod communities, humus systems, or soil coverage conditions.

(iv) To determine whether specific microarthropod taxa or humus forms may serve as indicators of habitat change

(v) To provide recommendations for the sustainable management of windthrow-affected areas with the goal of maintaining forest resilience.

Each of them is discussed below in light of the overall research findings.

(i) Characterize the various microhabitats resulting from windthrow damage in two Italian Alpine forests in terms of soil coverage and chemical soil parameters

Windthrow events introduce substantial heterogeneity into forest floors, primarily through localised alterations to soil covering conditions and the formation of canopy openings. Our findings indicate that these alterations act as the primary drivers of humipedon evolution following a windthrow disturbance.

In windthrow-affected areas, we identified three primary soil microhabitats: open areas with herbaceous vegetation cover, soil covered by various forms of decaying wood, and patches of bare soil.

Were all fallen trees were mechanically cleared or in the patches between fallen trees, the formation of canopy openings allows substantial solar irradiation to penetrate the forest floor. Five years after the disturbance, these areas are largely colonized by herbaceous vegetation, although some patches of bare soil persist.

Direct solar energy input on the forest floor raised temperatures, stimulated microbiological activity, increased soil respiration, and accelerated soil organic matter mineralization. This process has led to a reduction in the thickness of organic diagnostic horizons, a decrease in soil organic matter content, and an increase in pH within the upper 15 cm of the humipedon in open patches with herbaceous vegetation or bare soil. These modifications indicate that both herbaceous-covered soils and bare soil patches are gradually transitioning toward conditions characteristic of mountain permanent meadows.

Soil respiration rates and soil organic matter loss are greatest in bare soil, which represents the most extreme post-windthrow habitat. However, the extent of bare soil patches is limited and is gradually being colonized by herbaceous vegetation, implying the transition from bare soil to soils with herbaceous cover.

In contrast, coarse woody debris (CWD) accumulation on the forest floor—including fallen trees, branches, and logs—insulates the soil from direct solar exposure, reduces soil respiration rates, and slows organic matter turnover. Soils beneath deadwood exhibit thicker organic horizons, higher soil organic matter content, and lower pH levels, conditions similar to those of intact forest soils.

(ii) Study the evolution of humus profiles within these microhabitats and assess whether they correlate with soil coverage conditions.

Following the windstorm, humus composition evolved distinctly across various microhabitats, responding to the increased soil heterogeneity. As expected from the geology, the climate and the vegetation of the investigated areas, in intact forests, the dominant humus system is Amphi, characterized by thick organic horizons, notably in the Pachyamphi, Macroamphi, and Mesoamphi forms. The findings of some Leptoamphi and some Mulls underly the normal dynamical nature of the intact forest humipedon, where a normal heterogeneity is found at micro-site level, and it is essential for the forest regeneration dynamics. By contrast, permanent meadows largely exhibit Mull systems, with minimal variation.

The heterogeneity resulted from the windstorm results in an overall shift in the humus system, from a predominance of the Amphi system in intact forests to a gradual transition towards the Mull system in windthrow-affected areas, but with strong differences between the characterized microhabitats. In soils under herbaceous cover this shift is marked, and the analysis of the humus forms underly that if organic horizons persisted, they are thinner than that in the intact forests and that the humus is still evolving. Indeed, organic horizons are often thin and visibly biodisturbed, primarily by earthworms, bearing resemblance to Bipolar Amphi forms evolving toward Mull.

Increased sunlight exposure leads to more biologically active humus, higher decomposition rates, and consequently, faster mineralization of organic matter and its incorporation into the organo-mineral horizon. This process enhances nutrient availability and creates optimal conditions for the regeneration and growth of young trees, mirroring the natural dynamics observed in the Bipolar Amphi system in Alpine forest ecosystems. In this context, the Mull humus form represents a temporary phase that supports forest renewal, with catastrophic storms acting as triggers for the regeneration of mixed coniferous forests over varying spatial scales. However, the persistence of these new ecological conditions could, in the long term, drive a shift from forest to alpine meadow ecosystems.

In soil patches covered by coarse woody debris, the transition from Amphi to Mull is present but less pronounced compared to herbaceous-covered soils. Organic horizons under dead wood, even if disturbed, remain relatively thicker.

This progression poses potential challenges in the context of climate change, as rising temperatures may accelerate the shift from Moder to Amphi systems and from Amphi to Mull systems. These shifts imply fundamental changes in ecosystem functionality, with consequences for both vegetation and soil fauna composition.

(iii) Characterize the microarthropod communities within the same microhabitats and determine whether a discernible link exists between microarthropod communities, humus systems, or soil coverage conditions.

Microarthropod communities also evolve in response to the same drivers that shape distinct microhabitats within windthrow-affected areas. While community diversity indices remain stable in windthrow areas, suggesting a good resilience of the communities, a notable dissimilarity emerges across conditions, with communities in soils under dead wood and bare soils showing the highest divergence compared to the others.

Bare soils represent the most extreme post-windthrow habitat, being the only condition in which microarthropod abundance and diversity are significantly reduced. Here, no euedaphic microarthropod groups were recorded, with only the more mobile, epigeic groups persisting. This is the only condition in which a marked need for ecological recovery is evident, in terms of vegetation cover, biodiversity, and soil quality. Encouragingly, bare soil appears to be a transitory state, as it is largely colonized by vegetation five years post-disturbance, making it marginal yet important for understanding post-windthrow management implications.

In the other soil coverage conditions, microarthropod responses to disturbance were group-specific and varied based on sampling area and vegetation type.

Collembola appeared to benefit from the disturbance, with abundances under dead wood comparable to those in intact forest areas and even higher in soils with herbaceous cover. In contrast, Oribatid mites and Isopoda—typically associated with the organic-rich horizons of the Amphi humus system—were more sensitive to disturbance, showing a marked decline across all windthrow-affected patches. This characteristic makes them a potential good indicator for ecosystem damage. Protura group demonstrated to be the most dependent on vegetation litter and its abundance in intact forest was five time higher under deciduous vegetation than under coniferous vegetation. This can be explained by the trophic preference of the group, with a good number of species feeding on decomposing fungi, in which the broadleaf litter is rich. In fact, Protura seem to have benefitted by the presence of CWD on the forest floor, and the species composition has been enriched. Notably, as a confirmation to this hypothesis, a new Protura species, *Tuxenida lorenzoi*, was discovered in soil beneath decaying wood (Galli et al., 2025).

Given that the number of microarthropod groups and the total abundances did not significantly vary between soil coverage conditions, it is reasonable to say that a species-level community shift likely occurred within each microarthropod group. In soils beneath dead wood, the species compositions likely evolved toward a dominance of saproxylic species, living in the organic horizons and typical of Amphi humus systems. Additionaly, the species composition will likely vary again as the wood will reach subsequent decomposition stages. On the contrary, in soils under herbaceous cover communities likely shifted toward more heat-tolerant, herbivore, microbial grazer and predator species, living in the organo-mineral horizon typical of Mull humus system. It has been demonstrated that among the roles of microarthropods in litter degradation, it is of particular importance the release of disposable nitrogen during decomposition (Soong and Nielsen, 2016). It is reasonable to say that in the Mull humus systems under herbaceous cover, since microarthropods have decomposed almost all the remaining litter, there is, at this point, a higher concentration of nitrogen and other nutrients, that will contribute to create a favorable environment for the regeneration of the forest.

Despite the increased dissimilarity between communities in different soil conditions, no consistent link was observed between microarthropod communities and humus systems, which may depend on the methodology applied during the study.

It is known that different diagnostic horizons form through the activity of distinct soil organisms, and it was expected to find different communities in different humus profiles. But humus classification in windthrow areas proved to be a difficult challenge. In fact, OH and A horizons were often mixed, still undergoing a clear evolution or furthermore, with a thickness < 3 mm, and consequently not registered, resulting in horizons that did not align with typical humus system definitions. All these situations pose some challenges in the classification of the humipedon and therefore in finding a relation between humus systems and microarthropod community. As an example, in an Amphi evolving towards a Mull, an organic horizon is still present (that lead to the classification of that humus profile as an Amphi), but that horizon is functionally less “active”, as it is being “consumed”, and the animals dominating that humus profile are in fact the ones typical of Mull system, preventing to underly a potential associations between the entire humus profile and a specific microarthropod community.

It will be advisable, in further studies, to sample organic and organo-mineral horizon separately, to be able to link some arthropods to one specific horizon.

(iv) Determine whether specific microarthropod taxa or humus forms may serve as indicators of habitat change

In regard to the potential of using humus as an ecological indicator, this study confirms that humus system can effectively signal shifts in ecological dynamics, though its response time is notably slow, taking years to decades. The transition within the humus system unfolds more gradually than shifts in chemical soil parameters.

In the case of microarthropod-based indicators, no specific taxa were identified as correlating exclusively with one particular condition, except in Cansiglio forest, were Isopoda and Oribatid mites were associated to intact forest. Among these, Oribatid mites as a group have proved to be the most sensible group, confirming the existing literature on forest disturbances and attesting a decrease in abundances in all soil coverage conditions in windthrow-affected patches and expressing their potential to be considered as ecological indicators.
Regarding the community-based indicators, the QBS-ar index prove also in this study to be a reliable indicator of soil quality, demonstrating a positive correlation with all measured microarthropod parameters. However, it exhibited low sensitivity to shifts in the microarthropod community. While useful for broadly assessing forest damage and its resilience after a disturbance, it does not provide ecological insights into changes occurring within the communities.

(v) Provide recommendations for the sustainable management of windthrow-affected areas with the goal of maintaining forest resilience.

Based on findings from this research, several management recommendations can be made, in line with the existing bibliography on forest regeneration:

1. Given the importance of physical heterogeneity in supporting biodiversity, it is advisable to avoid applying uniform treatments across all windthrow-affected patches. This approach may involve clearing some areas while allowing others to regenerate naturally.
2. Retaining substantial amounts of coarse woody debris (CWD) on site—in the form of stumps, standing dead trees, and fallen logs and branches—can serve a multifunctional purpose. CWD supports saproxylic biodiversity, promotes forest regeneration, and functions as a long term reservoir of organic matter.
3. Where natural regeneration of windthrow patches is not feasible, management practices should aim to enhance the forest's inherent resilience to future windthrow events. This includes avoiding the establishment of uniform, single-species, and same-age stands, and instead promoting a mixed forest composition of broadleaved and coniferous species
4. Regarding the modeling of carbon stocks in forest soils, this study highlights the crucial importance of considering litter, which is sometime overlooked. In less metabolically active humus systems such as Moder, Amphi, and Tangel, litter represents the primary—and most fragile—reservoir of soil organic carbon.

In summary, windstorms do not inherently have a destructive impact on forest ecosystems. Rather, they play an integral role in the ecological dynamics of European forests, promoting forest regeneration and enhancing biodiversity. However, these processes unfold gradually. For example, humus continues to evolve five years post-disturbance, and full forest regeneration and the degradation of soil organic matter within coarse woody debris may span decades.

In this context, the critical role of CWD in forest regeneration, as a source of organic carbon, and as a biodiversity hotspot becomes increasingly evident. Serving as a unique and essential habitat, CWD supports diverse microarthropod communities, and protects soil from rapid organic matter turnover. This role is especially significant in European forests, where CWD is often systematically removed from the forest floor.

LIMITATIONS OF THE STUDY AND POSSIBLE FURTHER LINES OF RESEARCH

Several potential biases were identified during data collection, and we have taken measures to address them. Microarthropods are seasonal organisms strongly influenced by climatic conditions, making it challenging to obtain a fully representative sample of the entire community. Sampling was conducted in July, the optimal period for microarthropod collection in the Alpine region due to favorable temperature conditions. To ensure stable climatic conditions, all sampling was carried out over two consecutive weeks, avoiding periods of heavy rainfall. For continued monitoring and data comparability, future sampling should be conducted in the same season under similar optimal climatic conditions.

The microhabitat "soil under dead wood" exhibited the highest variability among sites, particularly in terms of dead wood type, thickness, and spatial coverage. To minimize variability, we exclusively sampled soils beneath dead wood with a minimum thickness of 20 cm, focusing on the central area to avoid potential edge effects at the ecotone between microhabitats.

A primary limitation of this study arose during data processing. As previously discussed, challenges emerged in accurately classifying disturbed diagnostic horizons and consequently, in classifying humus systems. This limitation may have obscured potential relationships between microarthropod communities and humus systems. A possible solution to address this issue in future research is to separate the sampling of organic and organo-mineral horizons, performing microarthropod extraction independently for each horizon. This approach, which bypasses humus classification, could more precisely reveal microarthropod dynamics within each horizon and help identify the key groups that drive the evolution of each horizon.

The second limitation was the taxonomic level of microarthropods identification, that was performed at quite high level. Although this approach allowed us to capture broader community dynamics and highlight increasing dissimilarity across the entire microarthropod community, it did not reveal finer shifts occurring within each microarthropod group. Investigating this aspect would require species-level identification within each group, a task demanding specific taxonomic expertise. Consequently, studying multiple groups at this level would necessitate collaboration among specialists, which could be a valuable focus for future research on microarthropod community dynamics following natural disturbances.

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