

The Necrobiome of Deadwood: The Life after Death

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Abstract: In recent decades, sustainable forest management has been increasingly recognized, promoting the diffusion of silvicultural practices aimed at considering all components of the forest system. Deadwood is an important component of the forest ecosystem. It plays a fundamental role in providing nutrients and habitats for a wide variety of saprotrophic and heterotrophic organisms and significantly contributes to soil formation and carbon storage. Deadwood is inhabited by a plethora of organisms from various kingdoms that have evolved the ability to utilize decaying organic matter. This community, consisting of both eukaryotic and prokaryotic species, can be defined as “necrobiome”. Through the interactions between its various members, the necrobiome influences the decay rates of deadwood and plays a crucial role in the balance between organic matter decomposition, carbon sequestration, and gas exchanges (e.g., CO₂) with the atmosphere. The present work aims to provide an overview of the biodiversity and role of the microbial communities that inhabit deadwood and their possible involvement in greenhouse gas (CO₂, N₂O, and CH₄) emissions.

Keywords: archaea; bacteria; ciliate; forest ecosystem; fungi; microbial diversity; wood decay

1. Introduction

Forest ecosystems host a large portion of terrestrial biodiversity and play a crucial role in the biogeochemical cycles of the elements, influencing the climate and providing ecosystem services for the well-being of society. Therefore, forest management actions for forest ecosystem preservation represent an important tool for biodiversity conservation and ecosystem functioning [1]. Sustainable forest management (SFM) has become a central guiding principle to preserve forest ecosystems' biodiversity and functionality, allowing the spread of management practices aimed at considering all forest components. Since the 1990s, the role and importance of deadwood in forest ecosystems have been recognized at a political level. Consequently, deadwood volume has become one of the most important indicators of forest biodiversity belonging to the Pan-European qualitative indicators for SFM [2], and it has been included within the list of the five carbon pools provided by the Intergovernmental Panel on Climate Change [3].

According to the Global Forest Resources Assessment 2005, forest deadwood can be defined as all non-living woody biomass not contained in the litter, either standing, lying on the ground, or in the soil [4] (Figure 1). Deadwood includes several components such as snags, standing dead trees (including high stumps), lying dead trunks, fallen branches, fallen twigs, and stumps [5].

In recent decades, the perception of the importance of deadwood in forest ecosystems has gradually changed. Consequently, forest management actions aimed at regulating the amount of deadwood in forests have been modified. In the past, non-living woody biomass present in forests was perceived negatively for health reasons, such as pests, insect attacks, [6] or greater risk of fires [7], and deadwood was generally removed during silvicultural operations. Nowadays, deadwood is recognized as an essential structural and functional component of forests [8], with a central role in sustaining forest biodiversity and delivering ecosystem services (ESs). It functions as a habitat for numerous plant and



Citation: Pastorelli, R.; De Meo, I.; Lagomarsino, A. The Necrobiome of Deadwood: The Life after Death. *Ecologies* **2023**, *4*, 20–38. <https://doi.org/10.3390/ecologies4010003>

Academic Editor: José Ramón Arévalo Sierra

Received: 2 November 2022

Revised: 14 December 2022

Accepted: 16 December 2022

Published: 22 December 2022



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animal species (Figure 2), an essential substrate for numerous insects [9] and fungi [10], a key factor in nutrient cycling [11], a fundamental element in the geomorphological and soil hydrological processes [12], and a valuable forest carbon pool contributing to climate change mitigation [13,14].



Figure 1. Deadwood: standing and lying trunks, fallen branches, and coarse wood debris.



Figure 2. Deadwood provides a favorable environment for the regeneration of plant species and natural shelters for animals.

The management of forests for timber and bioenergy production while maintaining and/or improving other ecosystem services has been one of the most significant research challenges since the concept of ESs was developed [15]. The amount of deadwood in a forest depends on a set of natural and anthropogenic variables: forest type, stage of forest development, local geo-climatic situation, and the kind and frequency of anthropogenic disturbances. In particular, the qualitative and quantitative presence of deadwood in a forest is influenced by both forest systems (coppice or high forest) and management intensity [16,17]. Silvicultural strategies play a crucial role in maintaining or increasing the volume of deadwood in forests. Thus, ad hoc solutions and the well-designed planning of different silvicultural actions may be fundamental to achieving a balance between forest productive functions and deadwood environmental benefits [17].

In forest ecosystems, most biodiversity, even at the intraspecific level, is found among bacteria, fungi, protozoa, lichens, and arthropods [18]. These organisms live mainly in the soil, but they are also abundant in the necromass (deadwood, litter, animal carcasses), where they are key actors in decomposition processes [19]. Two types of organisms, which depend on deadwood presence in the forest ecosystem, can be distinguished: (i) directly dependent organisms that use the deadwood as a substrate for germination, as a power source, or as a nesting site, and (ii) indirectly dependent organisms that occasionally find shelter in the coarse woody debris or in standing dead trees at either an early or advanced level of decomposition [20].

Considering the central role of deadwood in the biological diversity and functionality of forest ecosystems, studies concerning its typology and abundance, and the mechanisms involved in its decomposition, are of increasing interest.

2. The Necrobiome of Deadwood

The term necrobiome was originally used to describe “the community of species (e.g., prokaryotic and eukaryotic) associated with decomposing remains of heterotrophic biomass, including animal carrion and human corpses” [21]. This term, initially focusing mainly on vertebrate carrions, was later expanded by Benbow et al. [22] to include other forms of necromass, such as leaves, wood, and dung. Therefore, the term necrobiome can be associated with vegetable and animal necromass decomposition. Some aspects of the decomposing action of the necrobiome are common to all types of necromass, such as tissue disintegration, microbial activity, and the release and recycling of nutrients within the ecosystem. Conversely, other aspects are characteristic of each different form of necromass, such as community dynamics, decomposition rates, and specific decomposing taxa [22].

Deadwood is an important source of organic matter consisting of simple sugars, organic acids, and complex structural biopolymers such as cellulose, hemicellulose, and lignin. It is a crucial factor in nutrient recycling in forest soil [19]. In fact, through decomposition, the structural polymers of wood cell walls are demolished and transferred to the soil, making the nutrients contained therein available for soil microorganisms and absorption by plant roots [14].

The refractoriness of the lignin–cellulosic complexes is the main driver controlling the decay rate of deadwood. Only a limited number of fungi and prokaryotes possess the capability to decompose the lignin–cellulosic complexes, as they have developed the enzymes necessary to break them down [23]. The action of pedofauna, consisting mainly of invertebrates such as xylophagous insects (Figure 3), is fundamental in exposing a larger surface of the wood to microorganism attack. Through the chewing apparatus, the pedofauna fragment deadwood, favoring the mixing of organic molecules and soil mineral components [24].



Figure 3. The arthropods inhabiting deadwood contribute to its fragmentation.

Unicellular protozoa can also significantly contribute to mineralization processes and the recycling of the nutrients contained in deadwood [25].

The deadwood necrobiome is composed of organisms belonging to different kingdoms that have evolved to use decaying organic matter as a nutrient resource or as a habitat, interacting with each other through relationships that can be synergistic, antagonistic, and/or neutral [26]. Through these interactions, the necrobiome influences the deadwood decay rates and plays a crucial role in the balance between organic matter decomposition, carbon sequestration, and gas exchanges with the atmosphere (mainly carbon dioxide; CO₂) [27,28].

The necrobiome colonizes plant tissues immediately after or before their death and may have an internal (endonectrotic community) or external (epinectrotic community) origin [22]. Climate and the quality of the woody substrates (density, pH, moisture content, total lignin, and cellulose contents) are the driving forces of deadwood decomposition, as they strongly influence the structure of the necrobiome and the speed of the decomposition process [29,30]. As the woody material decays, its structure and chemical composition gradually change, inducing a succession of microbial communities, as species are progressively replaced by other species that are better adapted to the new habitat [31–36]. The incorporation on the soil surface organic layer of woody material at various stages of decomposition can have consequences on the chemical and biological properties of forest soil [37].

While it remains largely unclear which factors influence each group of organisms and to what extent, there is no doubt that deadwood offers a wide range of niches for many specialized organisms [38] and that its decomposition largely contributes to sustaining forest biodiversity [39].

2.1. Fungi

Fungi, in particular Basidiomycetes (Figure 4) and Ascomycetes, have always been considered pioneering microorganisms in the wood decomposition process [33]. Thanks to their ability to secrete various enzymes that attack the structural biopolymers of wood, fungi can readily colonize deadwood and modulate the availability of nutritional resources for their growth [23,33]. Furthermore, they promptly contribute to opening the way in the recalcitrant substrate for colonization by other microorganisms, including bacteria [40]. Several authors found that Ascomycetes are more abundant than Basidiomycetes, especially in the early phases of deadwood decomposition [28,33,41,42].

Endophytes are generally the first colonizing fungi [42]. Outside taxa preferentially take over in the later stages [43,44]. Fungi use two main colonization strategies: the dispersion of spores in the atmosphere and the invasion of mycelial filaments from the surrounding soil [45]. Following these stochastic events, the ability of certain fungal groups to degrade different substrates leads to temporary changes in the chemical composition of deadwood. As the state of decay progresses, a greater number of ecological niches become available to support the colonization of a highly diversified microbial community. As the wood decomposes, a greater variety of substrates gradually becomes available, requiring a greater metabolic diversity within the active bacterial and fungal communities [36,42].

Fungal taxa exhibit specific preferences for wood at a definite stage of decay [46]. Based on the different degradation strategies they operate, fungi are commonly classified into soft rot fungi, white rot fungi, and brown rot fungi. The soft rot fungi are mostly Ascomycetes and Deuteromycetes and are among the first colonizers [47,48]. They can degrade cellulose and hemicellulose, creating localized gaps that allow access to the necromass for other decomposing microorganisms. The term soft rot was originally proposed by Savory in 1954 [49] to distinguish the decay caused by these fungi, which attack only the cellulose, making the surface of the wood very soft, from the action of the white and brown rot fungi, which, conversely, destroy the wood [50]. White rot fungi and brown rot fungi are mainly taxonomically classified within the subdivision of Basidiomycetes [51,52]. White rot fungi secrete a plethora of extracellular oxidative enzymes capable of degrading all cell wall biopolymers [14,53]. They significantly reduce the lignin content of deadwood

thanks to the action of oxidative metalloenzymes, such as laccase and manganese peroxidase [23,54,55]. Some species preferentially remove the lignin, leaving white degraded areas mainly consisting of cellulose, while other species concurrently degrade lignin and cellulose [56]. After a first phase dominated by soft rot and white rot fungi, the decay process is predominantly driven by brown rot fungi, which can attack hemicellulose and cellulose, causing a relative increase in lignin [48,52]. They are not able to mineralize lignin into CO₂ and do not secrete peroxidase, but they apply a singular mechanism that uses hydroxyl radicals, produced by the non-enzymatic Fenton reaction, as an oxidizing agent [23,52]. Therefore, the lignin is modified while maintaining its polymeric structure [52]. Despite having limited ligninolytic activity, brown rot fungi are good competitors and are abundant in the late stages of deadwood decomposition [31,52,57].



Figure 4. Deadwood as a substrate for the growth of Basidiomycete fungi.

Hypoxylon frangiforme and *Lopadostoma turgidum* were found almost exclusively on deadwood at early stages of decomposition while *Trechispora farinacea* and *Phanerochaete velutina* were more frequently isolated from deadwood at late decay stages [58]. A key player in Norway spruce decomposition is *Guehomyces pullulans*, which is very efficient in conquering the habitat in the early stages of decomposition and, successively, as the decay progresses, providing its biomass to feed other species [42]. The white rot fungus *Phlebia radiata* proved to be an efficient early colonizer of deadwood, contributing to wood decomposition by the secretion of oxidative and carbohydrate-active enzymes [23]. In Norway spruce deadwood, these enzyme activities were associated with the emission

of volatile organic compounds (VOCs), such as methyl-3-furoate [23]. Fungal VOCs are considered important signaling molecules in hyphal interspecific interactions.

Several species, such as *Eutypa spinosa* and *Fomes fomentarius*, have been identified as endophytes latently present in the living sapwood of the European beech [59]. They can utilize the available nutritional resources early, before the entry of secondary and late colonizers who may be stronger competitors [60]. Other examples of late colonizers are *Mycena haematopus* and *Pluteus* spp. [57]. The species *Resinicium bicolor* (Hymenochaetales), *Fomitopsis pinicola* (Polyporales), and *Heterobasidion* spp. (Russulales) have been found in the deadwood of conifers (*Picea abies*) in temperate and boreal forests [61–63]. *Trametes versicolor* (Polyporales) and members of *Xylariales* have frequently been found in European temperate beech and oak forests. *Resinicium* spp. have been considered functional and structural key members of the necrobiome and are abundant in deadwood of both deciduous and coniferous species [64].

Furthermore, Mucoromycota were found in a significant percentage (11%) in Norway spruce deadwood blocks, almost exclusively referring to the genus *Mucor* [42]. Although this phylum is not considered a typical deadwood decomposer, it is presumed to be involved in facilitating the breakdown of complex sugars [57].

2.2. Bacteria

Bacteria are also involved in the deadwood decomposition process [65] (Figure 5). They colonize deadwood in early decay stages growing on easily degradable substrates such as sugars, organic acids, pectin, and easily accessible cellulose. In recent years, it has been shown that even bacteria can degrade wood's structural biopolymers, including lignin, and catabolize secondary products deriving from lignin's incomplete degradation by fungi [66,67]. However, their role in cellulose and lignin decomposition is lesser than that of fungi. Tláskal et al. [65] found that more than 91% of the transcripts involved in the degradation of structural wood biopolymers were of fungal origin, while only 7% were assigned to bacteria. By using a gene-centric approach, selecting 60 enzyme-encoding genes putatively involved in lignin depolymerization and the metabolism of lignin-derived aromatic compounds, Díaz-García et al. [67] predicted that some species within the Pseudomonadaceae family could possess broad and relevant ligninolytic activity.

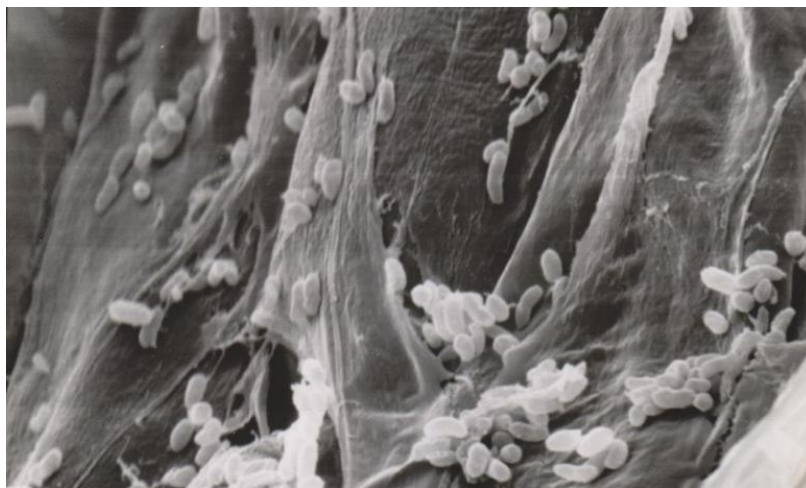


Figure 5. Bacterial cells colonize dead plant tissue (scanning electron microscope photo, 2620× magnification).

In 1971, Greaves [68] first conceptualized a functional classification of bacteria inhabiting deadwood: (i) bacteria that affect permeability but do not significantly alter the strength of the wood material, (ii) bacteria that affect the wood strength properties by attacking wood structures, (iii) bacteria that act as synergistic members of the total microflora, contributing to the ultimate deadwood breakdown, and (iv) “passive” bacteria, which can act

as antagonists to other bacteria. Bacterial pectinases play a key role in increasing wood permeability [69].

Based mainly on electron microscope ultrastructural observations, three main types of bacterial decay, clearly different from those operated by fungi, have been recognized: erosion, tunneling, and cavitation [56]. The erosion bacteria degrade the cellulose and hemicellulose of the secondary walls, producing deep channels parallel to the cell-wall microfibrils and leaving lignin residues. The tunneling bacteria produce tiny tunnels in the secondary walls and medium lamellae. The cavitation bacteria form small diamond-shaped or irregular cavities in the secondary wall [56]. While tunneling bacteria appear to require the presence of oxygen for their activity, erosion bacteria can tolerate conditions of extremely low oxygen levels [70].

Most deadwood saproxylic bacteria belong to the Proteobacteria, Actinobacteria, and Acidobacteria phyla [71]. They participate in the whole deadwood decay, being able to use a wide variety of more or less labile substrates and interacting with fungi through complex synergistic and competitive relationships [72–74]. *Bradyrhizobium* and *Caulobacter* were found to be the most frequent proteobacterial species in deciduous temperate mixed forest ecosystems [28]. The presence of *Bradyrhizobium* could potentially contribute to N-enrichment, thanks to its nitrogen (N_2)-fixing activity [28].

Deadwood is a favorable environment for the growth of actinobacteria. Many actinobacterial species can secrete cellulases and hydrolytic enzymes that degrade cellulose and hemicellulose [72]. Furthermore, they are presumably also involved in lignin degradation [75], although their role is not yet clear. Lynd et al. [76] retain the actinobacteria as early colonizers of deadwood; thanks to their cellulolytic action, they contribute to increasing the permeability of water and the humidity of the wood, thus favoring fungal colonization [77]. On the other hand, in the more advanced stages of decomposition, a greater metabolic specialization is hypothesized for actinobacteria, thus confirming their limited ability to degrade lignin [78]. Pastorelli et al. [36] found a greater number of actinobacterial taxa in the early stages of deadwood decay than in the more advanced phases. This finding suggests a greater involvement of this bacterial group in the degradation of more labile structural compounds, such as hemicellulose and cellulose, compared to more recalcitrant compounds, such as lignin.

Although the cultivation of the acidobacterial group has proved to be challenging, some members belonging to subdivision 1 have been isolated from deadwood colonized by the white rot fungus *Hypholoma fasciculare* [73]. Subdivision 1 hosts acidobacteria preferring a moderately acidic pH range [79] which are, therefore, presumably well adapted to the deadwood environment. By using an Illumina MiSeq platform, Lee et al. [28] identified *Terriglobus* as the most cosmopolitan species in the acidobacterial deadwood community. Acidobacteria have been described as abundant in the forest soil methylotrophic community [80]. However, their physiology and role in deadwood decomposition are still poorly known.

A significant portion of the deadwood prokaryotic necrobiome consists of bacteria capable of using reduced carbon substrates without CC bonding, such as methanol, a by-product of the lignin decomposition operated by fungi [65]. Vorob'ev et al. [81] identified the presence of methylotrophic microorganisms in association with the *H. fasciculare* fungus, in decaying beech wood. The obligate methanotroph *Methyloferula* sp. was found in association with *Amelanchier arborea* deadwood [28]. The group of methylotrophic bacteria also includes members with the ability to oxidize methane (CH_4), the so-called methanotrophic bacteria. In a mesocosm experiment performed on *Pinus nigra* deadwood fragments, methanotrophic bacteria increased with increasing decay class and CH_4 consumption, suggesting relatively greater involvement of this microbial group as decomposition progresses [36]. Mäkipää et al. [82] found methanotrophs as the main group within the N_2 -fixing prokaryotic community in spruce deadwood. They assumed the presence of synergistic interactions between methanotrophs and fungi, with the former providing ammonium (NH_4^+) to the fungi in return for the methanol produced by the latter [83].

Nitrogen-fixing bacteria also significantly increase as decomposition progresses [36,84]. Using a meta-transcriptomic approach to analyze the microbiome associated with European beech deadwood decay, Tláskal et al. [65] found that N_2 -fixation is one of the dominant processes of the N cycle occurring in deadwood, second only to the incorporation of NH_4^+ into organic molecules. On the contrary, the respiratory pathway (denitrification) that reduces nitrates (NO_3^-) and nitrites (NO_2^-) seems to be considerably less important in deadwood than in soil, and the transcripts related to the nitrification process were absent. Denitrifying bacteria are abundant and widespread in forest soils [27]. Denitrification is a stepwise process that involves several enzymes (reductases) and results in the conversion of dissolved NO_3^- and NO_2^- to molecular nitrogen (N_2), passing through the production of nitrous oxide (N_2O) [85]. Not all denitrifying bacteria harbor the complete battery of genes encoding for all the reductases of the denitrification process. Some denitrifying species have a truncated metabolic pathway [85]. Pastorelli et al. [36] quantified two key denitrification genes, the *nirK*, and *nosZ* genes, and N_2O potential emission from black pine deadwood. The obtained results suggested that the deadwood necrobiome may host a diversity of species that could drive denitrification towards a complete reduction in nitrate up to the release of N_2 , thus lowering N_2O emissions.

The *amoA* gene involved in NH_4^+ oxidation, the first step of the nitrification pathway, was detected only at low levels both in the bacterial and archaeal communities of deadwood [36,65]. Little is known about the role of this group of prokaryotes in wood decomposition. They are also involved in N_2O emissions [86], but their contribution to deadwood appears potentially less relevant than that of denitrifying bacteria.

2.3. Archaea

Little is known about the metabolic activities of the prokaryotes belonging to the Archaea domain and their involvement in deadwood degradation. Enzymes such as cellulase and xylanase have been discovered in extremophilic archaea [87], but it is not known whether these enzymes may also be present in temperate archaea [88].

Numerous members of this domain can produce CH_4 as a metabolic by-product. The CH_4 emission is the result of the activity of a consortium of microorganisms, where simple C-compounds are produced by the degradative and/or fermentative activity of other microorganisms and used as terminal electron acceptors by methanogenic archaea [89]. The colonization of living tree tissue by methanogenic archaea was documented as early as the 1970s [90]. The early stages of decomposition showed the highest methanogenic activity [91]. This finding suggested that methanogenesis is fueled by non-structural labile C substrates, most abundant in less-decayed wood [91]. Fungi break down cell structural biopolymers, generating by-products that other wood microorganisms may use to produce CO_2 and H_2 , primary substrates for the methanogenesis process [92]. However, non-methanogenic archaea have also been found in decaying wood, indicating archaea as integral and dynamic members of the plant necrobiome [88].

To date, Thaumarchaeota have been found as prominent members of the archaea community of forest necromass, highlighting the versatility and cosmopolitan nature of this phylum in the natural environment [88]. However, it is easier to assume that CH_4 evolution occurs mainly as a result of symbiotic interactions between methanogenic archaea and xylophagous insects, protozoa, or fungi inhabiting the deadwood [92–94]. In a mesocosm experiment conducted on *P. nigra* deadwood, Pastorelli et al. [36] found the presence of *Methanobrevibacter* strongly correlated with the high production of CH_4 (Figure 6). *Methanobrevibacter* is a strictly anaerobic species that generally live as a symbiote of protozoa or are attached to the intestinal epithelium of both lower and upper termites. Furthermore, a great abundance of *Methanobrevibacter* has also been found within the cells of *Spirotrichonympha leidy*, a flagellate of the parabasalid group that lives in the termite intestine [94].

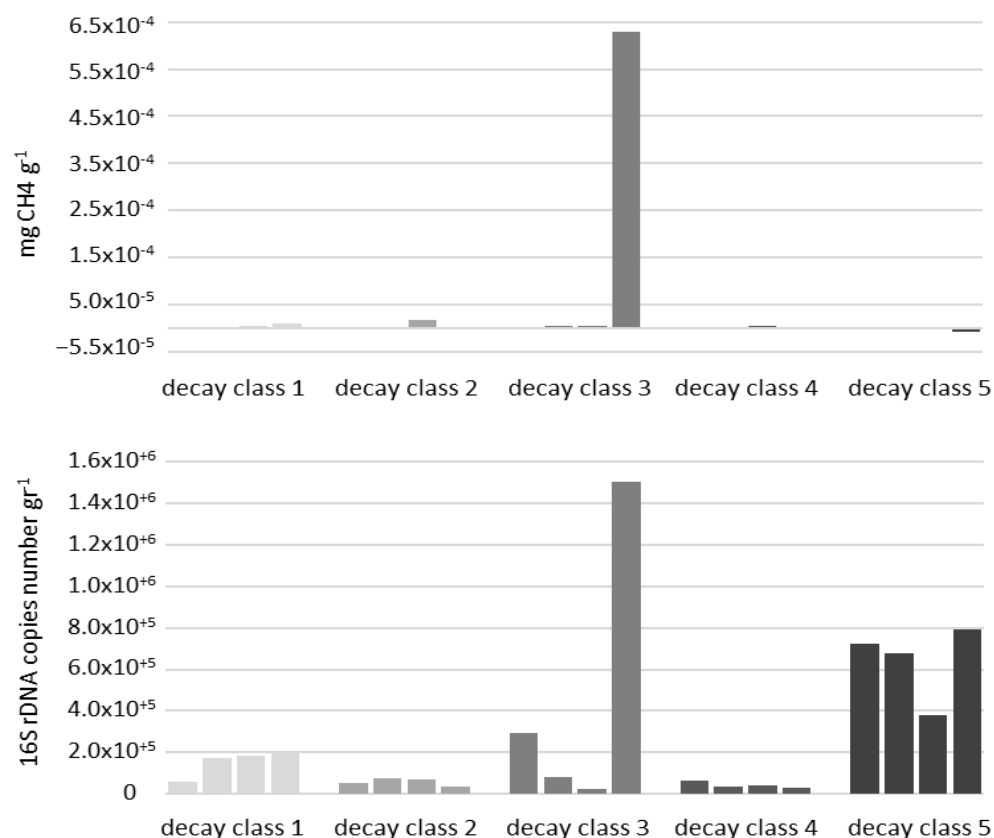


Figure 6. Maximum values of CH_4 production and number of methanogenic archaeal 16S rDNA gene copies resulting from a mesocosm experiment consisting of the cores of five different decay classes from black pine (*Pinus nigra* J.F. Arnold) lying deadwood. The sequence analysis conducted on the sample with high CH_4 emission showed a great abundance of *Methanobrevibacter* [36].

2.4. Ciliate

Ciliophora is one of the most abundant phyla of the protozoan community in soil, but ciliates can also inhabit mosses, lichens, litter, and deadwood [95,96]. Ciliates are important members of the ecosystem trophic network since they prey on microorganisms and are preyed upon by other protozoa and metazoans, thus playing a very central role in nutrient recycling [95]. Understanding ciliate functions and diversity is essential to extending our knowledge about the nutrient cycle in forest ecosystems. However, most ecological studies on this group of protozoa have been conducted on the soil, and reliable data on their abundance and taxonomic composition in deadwood are still scarce.

Different ciliate species have specific food preferences and tolerate specific microclimates and abiotic conditions [96]. Ciliates are highly adaptable to environmental changes and, thanks to their ability to develop inactive forms (cysts), they can survive adverse conditions [97], such as wet–dry alternations. Pastorelli et al. [98] showed that, like the other members of the necrobiome, the composition of the ciliate community varies as deadwood decays, becoming more and more homogeneous (Figure 7). The early stages of deadwood decomposition are characterized by great variability in deadwood quality, probably due to stochastic events that led to colonization by bacterial and fungal taxa with different degrading capacities [45] and ciliate taxa with different food preferences. As the decomposition progresses, the bacterial, fungal, and ciliate taxa are mainly selected according to deterministic mechanisms [99] controlled by the metabolic processes involved in the degradation of complex wood residues and by the palatability of the degrading microorganisms [19].

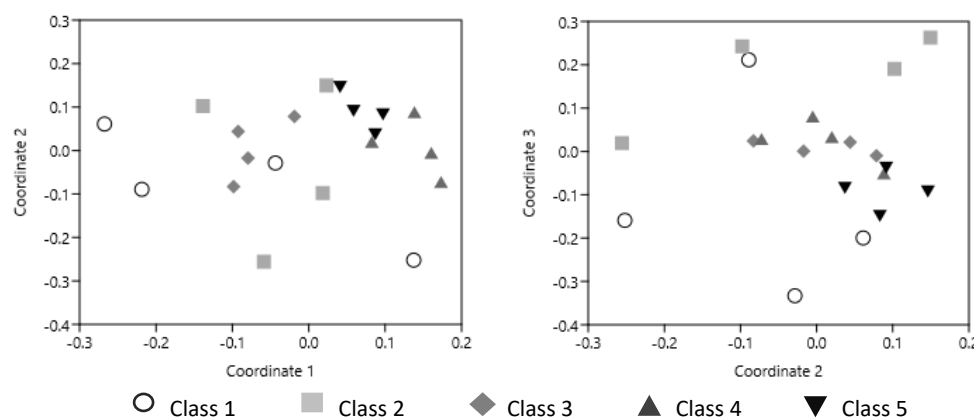


Figure 7. nMDS ordination plots of ciliate 18S rDNA gene obtained by PCR-DGGE from black pine deadwood at different decay classes [98].

Ciliates are ubiquitous and can be easily dispersed in the air [97]. They are susceptible to a wide range of environmental factors, such as humidity, temperature, pH, and food abundance, which can induce changes in their community composition [100,101]. Since ciliates need water to be active, the daily fluctuations of temperature and humidity can induce cycles of encystment and excystment so that, due to the different tolerance to abiotic conditions and food preferences, at any moment the habitat is occupied by active and inactive individuals [96].

The ciliate trophic groups in deadwood are very similar to those in soil with the prevalence of bacterivores and predators in the most decomposed deadwood [102]. Through the predation and secretion of metabolites, ciliates regulate the size and composition of bacterial communities and influence C and N cycling [19]. The nutrients temporarily immobilized in the bacterial biomass are released by the ciliate predatory action. Overall, deadwood ciliates affect the rates of nutrients released into the soil and atmosphere and significantly contribute to improving plant growth [100]. Part of the ingested C is used for new ciliated biomass production while the rest is returned to the atmosphere as CO₂. Organic molecules not used by any species of fungi, bacteria, or ciliates become a non-recycled end-product and accumulate in the soil, contributing to humus formation [96]. Nitrogen excesses are excreted as NH₄⁺, readily available to other organisms, improving the total N content of deadwood and soil fertility [100]. Consistently, the abundance of ciliates in deadwood was found to be positively correlated with CO₂ production, N content, and bacterial abundance [98].

The ciliate species identified in deadwood generally belong to soil-inhabiting genera within the Colpodea and Spirotrichea classes [98]. Colpodea are abundant in soils, especially in polluted soil [103,104], and are typically bacterivorous [95]. Interestingly, Jia et al. [19] showed a vesicular Colpodea strongly related to catalase and polyphenol oxidase, both enzymes involved in the degradation of refractory C sources, such as lignin. This finding suggested a potential role of Colpodea in deadwood degradation. Spirotrichea are common in soil, freshwater, and marine environments. Bartošová and Tirjaková [102] identified Colpodea, Spirotrichea, and Lithostomes as dominant systematic groups in decaying bark and wood.

3. Factors Affecting Decomposition

The wood–soil contact enhances the ability of the necrobiome to colonize deadwood by facilitating the microbial species to move from soil to wood residues and by increasing the deadwood’s moisture [105]. Jaroszewicz et al. [106] found that the composition of fungal assemblage strongly depends on the degree of deadwood debris’ contact with soil (on the ground, underground, or aboveground). Several studies on Mediterranean forests have shown that humidity has a higher influence on the activity of enzymes such as

endoglucanase, cellulose, and peroxidase than temperature. The activity of these enzymes is strongly correlated to cold/hot or humid/dry alternations, typical characteristics of the Mediterranean climate [107].

Baldrian et al. [108] found high variability in deadwood chemistry with the general trend of increasing N content and decreasing pH as decomposition progresses. The N content appears to be a factor that significantly affects the composition of the fungal community. In the early stages of decomposition, the low wood N content represents a more important and limiting factor for fungal growth than the recalcitrance of structural biopolymers such as lignin.

Many saproxylic fungi are host-specific, e.g., *Fomitopsis rosea* and *Daedalea quercina* exhibited preferences for spruce and oak deadwood, respectively. Furthermore, several taxa have a distinct predilection for deadwood from gymnosperms or angiosperms [106]. Alongside decomposition, deadwood undergoes changes mainly related to the reduction in density and the accumulation of nutrients and lignin compounds [29,57]. The rate of density reduction depends on the wood's initial density and varies according to the tree species [107], as different species contain different concentrations of structural compounds such as lignin. Lignin represents a barrier to wood degradation because it protects cellulose and hemicellulose from microbial attack [109]. By degrading lignin, the specialized ligninolytic microorganisms (Basidiomycota and some Ascomycota) increase the accessibility of the non-ligninolytic microorganisms to the other structural carbohydrates [109]. In conifers, the wood density decreases more slowly than—for example—in birch, which decomposes completely in a rather short period of about 25–40 years [110]. In natural boreal forests, *Picea abies* wood density is considered an indicator of the rate of decomposition [108]. The composition of the woody debris of broad-leaved species differs considerably from that of conifers [32]. Deciduous trees generally have high-quality organic components, with a higher nutrient content, the presence of more labile compounds, and a lower concentration of lignin and polyphenolic compounds than conifers [32]. Therefore, the woody structure of broadleaf trees is better suited to promote the faster decomposition of wood residues [107]. *Fomitopsis rosea* and *Xeromphalina campanella* have been proposed as saproxylic indicator species for spruce and general conifer deadwood, respectively [106]. *Daedalea quercina*, *Peniophora quercina*, *Panellus stipticus*, *Xylobolus frustulatus*, *Jackrogersella multiformis*, and *Hymenochaete rubiginosa* have been hypothesized as saproxylic indicator species for the deciduous oak and hornbeam [106]. Lee et al. [28] suggested that fungal taxa may be more specialized to a specific wood substrate than bacterial taxa. The substrate specificity expressed by the bacterial and fungal species is more evident in the early stages of decomposition than in the late ones, suggesting the progressive homogenization of woody substrates as the decay proceeds [28].

Furthermore, concerning the relation between C concentration and decomposition, C content can vary within individual trees and between species [111]. Deadwood has a high initial C/N ratio which tends to decrease during decomposition because of N inputs due to fungal N translocation [65], N₂-fixation by bacteria [112], and N secretion by protozoa [100,101]. Carbon concentration increases during the decay process with the loss of polysaccharides and the related accumulation of lignin during the decay process [113]. However, in some cases, the percentage of C may not differ significantly between the decay classes. Potassium is released faster than other nutrients by leaching, but it is also subject to immobilization by microorganisms, while the concentration of phosphorous increases with a species-specific pattern [114].

4. Interspecific Interactions within the Necrobiome

Within the necrobiome, various microbial members can coexist, interact, and influence each other. Numerous intra- and inter-specific interactions occur within the forest necrobiome. The efficient cellulose-degrading *Trichoderma* species may benefit from the delignification process carried out by white rot fungi [42]. On the other hand, by covering naked wood, fungi belonging to *Sistonema* and *Resiniium* spp. may slow down the

development of other fungal species and hinder the xylophagous invertebrate deadwood colonization [106].

During the deadwood decomposition process, both mutualistic and antagonistic interactions have been observed. These interactions are the driving forces of the functioning of nutrient recycling [115,116]. By degrading the structural biopolymers of deadwood, fungi weaken the lignin barriers and release readily degradable oligomers, providing opportunities for bacterial cell access and growth [117]. At the same time, bacteria can also make wood more accessible to fungi [118], particularly in the early stages of decomposition. Fungi could also facilitate colonization by soil bacterial cells adhering to their exploratory hyphae [73]. On the other hand, the decomposition processes operated by fungi lower the pH and generate reactive oxygen species, creating an adverse and selective environment for bacterial colonization [54]. It has been found that the white rot fungi *H. fasciculare* and *R. bicolor* can produce toxic compounds, sesquiterpenoid antibiotics, with bactericidal and/or bacteriostatic effects that counteract the deadwood colonization by bacteria or reduce the number of bacteria that have already colonized it [73]. Bacteria can also have negative effects on the fungal community by competing for low-molecular-weight nutrients. On the other hand, bacteria provide fungi with limiting nutrients, such as N (through N₂ fixation), and growth factors, such as vitamins [54]. Furthermore, bacteria can detoxify the deadwood environment by eliminating fungal growth inhibitory compounds [116]. Fungi may meet their N needs for vegetative and generative growth through association with N₂-fixing bacteria. In the deadwood logs of *Fagus sylvatica* and *P. abies*, Hoppe et al. [84] found positive correlations between fungal sporocarps and the abundance of *nifH* genes (coding for dinitrogen reductase, a key enzyme in the N₂-fixing process). Along the same lines, Gómez-Brandón et al. [42] observed that in *P. abies* coarse woody debris at different stages of natural decay, the abundance of fungi was strongly correlated with the abundance of *nifH* gene copies.

All the organisms inhabiting deadwood contribute in some way to transforming the debris of autotrophic origin and introducing the released nutrients and organic matter into the trophic network of the forest ecosystem. The term “microbial loop”, or microbial chain, proposed by Azam et al. [119], describes the process that acts as a link between necromass and the classical trophic network, ensuring the recycling of nutrients and energy contained in the organic matter [100]. Bacteria and fungi are primary saprotrophs. By degrading the structural biopolymers of wood, they contribute to the release of nutrients [96]. A certain number of primary saprotrophic taxa is necessary to provide a diversity of enzymes degrading the various wood substrates and to occupy the different microhabitats characterized by a variety of environmental conditions. Fungal and bacterial number and activity increase as decomposition progresses. In the late decay classes, most of the deadwood biomass is immobilized within their biomass, in particular as cell wall molecules (chitin and murein, respectively) [96]. Primary saprotrophs are preyed upon by secondary saprotrophs, including specialized ciliates [102]. Fungivores and bacterivores digest the primary saprotrophs and transform these cells and their walls into new biomass. Thus, biomass is transferred to a subsequent trophic level. Therefore, the increase in bacteria and fungi is followed by an increase in ciliate predators [98]. Different species of ciliates have specific food preferences, thus influencing the dynamics of bacterial and fungal communities and, consequently, the expression of genes encoding for enzymes associated with decomposition [19].

The microbial chain that develops in deadwood promotes the mineralization of organic matter, increases the availability of nutrients (C, N, P, and S), and supports plant growth [96,100]. The transfer of nutrients to plants through the predation of microbial biomass by ciliates has been demonstrated in numerous studies. In the plant rhizosphere, ciliates can mobilize about one-third of the consumed N as NH₄⁺ by consuming rapidly growing bacterial biomass [120].

5. Role of the Necrobiome in Climate Change

Deadwood represents a significant fraction of the forest C stock, accounting for 10–20% of the total C pool in mature forests [121]. However, this C pool is transient because, through the transformations operated by saproxylic microorganisms, it is released into the atmosphere mainly as CO₂, while the rest is transferred to litter, leached in soil water, or sequestered in the soil [65]. Therefore, microorganisms play a crucial role in maintaining the balance between the decomposition of organic matter and C sequestration in forests [27]. The double role of deadwood as a sink and source of C has a high impact on biogeochemical cycling and climate change [122]. Deadwood decomposition, together with forest fires, is one of the main processes that release CO₂ from the earth's surface with strong implications for temperature increases. In situ measurements of CO₂ emissions from deadwood highlighted an increase in deadwood respiration correlated with the progression of decomposition and bacterial abundance [35] (Figure 8).



Figure 8. Portable infrared gas analyzer operating in closed-path mode for the in situ measurement of CO₂ production from deadwood [35].

Climate change is expected to alter forest species distribution, particularly at higher latitudes and altitudes, affecting groups of decomposers that colonize specific forest species [123]. Where temperature is a limiting factor, climate warming can increase forest productivity, leading to the increased storage of C [124]. However, microbial activity, the faster decomposition of organic matter, and net CO₂ release are expected to increase as temperatures rise. Microbial activity increases under high CO₂ concentrations, favoring a more rapid decomposition of the organic substance [125].

Climate changes are also believed to affect N dynamics in forests, in particular in boreal ecosystems. A slight increase in N availability could improve deadwood decomposition by influencing the response of fungi forming mycelial cords [126]. However, other studies have shown that an N excess can reduce the activity of fungal ligninolytic enzymes [127]. Higher temperatures may also cause an acceleration of the nitrification and denitrification processes [27]. Denitrification is a process that leads to N₂O emissions operated by bacteria widely distributed in the environment and showing high taxonomic diversity [85].

Deadwood can also be a significant source of CH₄ emissions [34,36,128]. The production of CH₄ is mainly the result of deadwood decomposition mediated by members belonging to the archaea domain (Figure 6). Recently, brown rot fungi have been also identified to produce CH₄ under anaerobic conditions [129].

However, there is currently little understanding of the relationship between microbial diversity and deadwood decomposition. All the information obtained on the microbial species or functional groups involved in the decomposition processes is of fundamental importance for the prediction of the responses of forest ecosystems to climate change. New

data are needed to help in clarifying the processes that regulate global warming and the flows of greenhouse gases from deadwood [130].

6. Conclusions

New knowledge on the deadwood necrobiome is of critical importance to improve forestry strategies for deadwood management during silvicultural operations. In fact, during the mechanical operations of harvesting deadwood, only the trunks in the first stages of decomposition are generally taken away, because the removal of the most decomposed trunks is difficult. By adopting the principles of naturalistic forest management, an amount of 20–50 m³ ha^{−1} of deadwood should be preserved, preferably concentrating in networks of senescence islands (1–2 ha each) with an equal distribution by decay classes. Forest managers should consider this aspect to maintain and improve biodiversity in managed and semi-natural forests.

Author Contributions: Conceptualization, R.P., I.D.M. and A.L.; writing—original draft preparation and reviewing, R.P., I.D.M. and A.L. All authors have read and agreed to the published version of the manuscript.

Funding: The work was financially supported by the LIFE program, in the context of FoResMit (LIFE14/CCM/IT/905) “Recovery of Degraded Coniferous Forests for Environmental Sustainability Restoration and Climate Change Mitigation” and SelPiBio (LIFE13 BIO/IT/000282) “Innovative silvicultural treatments to enhance soil biodiversity in artificial black pine stands, i.e., for demonstration of innovative silvicultural treatments in artificial black pine stands” projects.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All data for the review are from the original publications, which can be found in the reference list.

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

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