Understanding the influence of abiotic factors on deadwood processes and deadwood-inhabiting fungal diversity: A focus on microclimate effects

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“The clearest way into the Universe is through a forest wilderness.”

— John Muir, 1890

ZUSAMMENFASSUNG

Der globale Klimawandel beeinflusst Waldökosysteme sowohl direkt (z. B. durch Temperaturanstieg) als auch indirekt (z. B. durch Störungsereignisse wie Windwürfe). Diese Veränderungen wirken sich auf die Struktur und Prozesse von Waldökosystemen aus, einschließlich Totholz, das wichtige Lebensräume bietet und zentrale Ökosystemfunktionen unterstützt. Der Abbau von Totholz spielt eine entscheidende Rolle bei der Regulierung von Kohlenstoff- und Nährstoffkreisläufen in Wäldern. Dieser Abbau wird jedoch durch ein komplexes Zusammenspiel zwischen Umweltbedingungen und holzabbauenden Organismen beeinflusst. Klimawandelbedingte Störungen wie Windwürfe führen, sofern das Forstmanagement das Holz nicht entfernt, zu einer Zunahme von Totholzmenge und -vielfalt, während sie gleichzeitig durch den Baumkronenverlust das Mikroklima im Bestand verändern. Diese Veränderungen können die Zersetzung von Totholz und damit verbundene Prozesse beeinflussen. Studien haben gezeigt, dass das Mikroklima ein wichtiger Faktor ist, dass sowohl die Abbaurate als auch die Artzusammensetzung der Zersetzergemeinschaften direkt beeinflussen kann.

Dennoch bestehen erhebliche Wissenslücken beispielsweise darüber, wie Umweltvariablen auf Bestandes- und Objektebene die innere Totholztemperatur und damit möglicherweise auch die Besiedlung und Aktivität von Zersetzern, wie totholzzersetzende Pilze, beeinflussen. Zwar ist bekannt, dass das Mikroklima auf Bestandsebene die Vielfalt holzzersetzender Pilze beeinflusst, jedoch sind die Folgen langfristiger mikroklimatischer Veränderungen auf die Sukzession von Pilzgemeinschaften weitgehend unbekannt. Ebenso ist das Zusammenspiel zwischen abiotischen Faktoren, Pilzdiversität und deren kombinierter Einfluss auf Zersetzungsprozesse bislang unzureichend verstanden. Die meisten Studien untersuchten bisher die Effekte von Umweltparameter oder Pilzdiversität auf Totholzzersetzung isoliert und vernachlässigten dabei die indirekten Effekte der Umwelt auf die Beziehung zwischen Pilzdiversität und Zersetzung. Zur Schließung dieser Wissenslücken analysierte ich Daten eines Langzeit-Totholzexperiments, dass 2011 im Nationalpark Bayerischer Wald eingerichtet wurde.

Im ersten Teil meiner Dissertation untersuchte ich, wie Faktoren auf Bestandesebene (Baumkronenöffnung, umliegende Totholzmenge) und Objektebene (Baumart, Totholzdurchmesser, Position) die innere Temperatur von Totholz beeinflussen. Die Kronenbedeckung erwies sich als der wichtigste Faktor: In offenen Beständen waren während der Vegetationsperiode (Mai-Oktober) Tagesmitteltemperatur und Tagesmaximumtemperatur

höher, während die Tagesminimumtemperatur niedriger war als in geschlossenen Beständen. Im Winter (November-April) führten offene Bestände zu niedrigerer Minimumtemperatur im Totholz. Insgesamt lag die mittlere Jahrestemperatur im Totholz unter offenen Baumkronen um etwa 1 °C (Mittelwert) bzw. 5 °C (Maximum) höher und etwa 2 °C (Minimum) niedriger als unter geschlossenen Baumkronen. Die weiteren Faktoren hatten schwächere und weniger konsistente Effekte auf die Temperatur. Diese Ergebnisse deuten darauf hin, dass die klimawandelbedingte Zunahme von Windwürfen und die dadurch verursachten Kronenstörungen die Temperaturverhältnisse im Totholz verändern und somit die Lebensbedingungen totholzzersetzender Pilze sowie die damit verbundenen Abbauprozesse beeinflussen könnten.

Im zweiten Teil analysierte ich, wie sich das Mikroklima auf Bestandesebene auf die Sukzession und die Zusammensetzung der Artengemeinschaft von fruchtkörperbildenen Pilzarten auswirkt. Über einen Zeitraum von zehn Jahren konnte eine zunächst ansteigende, später abnehmende Diversität an Arten beobachtet werden, wobei der Rückgang unter offenen Baumkronen deutlicher ausfiel. Die Zusammensetzung der Artengemeinschaften unterschied sich zwischen offenen und geschlossenen Baumkronen und blieb über die zehn Jahre relativ stabil, wobei etwa 25 % der Pilzarten ausschließlich unter einer der beiden Baumkronenbedingungen vorkamen. Diese spezialisierten Arten besiedelten jedoch weniger Totholzobjekte als Arten, die in beiden Bedingungen auftraten. Die Ergebnisse deuten darauf hin, dass die Sukzession der totholzzersetzenden Pilze eine gewisse Resilienz gegenüber mikroklimatischen Veränderungen zeigt, vermutlich durch artspezifische Toleranzen oder Spezialisierungen.

Im dritten Teil der Dissertation analysierte ich, inwiefern Umweltbedingungen und Pilzdiversität die Abnahme von Totholzdichte (Proxy für Zersetzung) beeinflussen. Dabei wurden sowohl die direkten Einflüsse der Pilzdiversität und der Umwelt auf die Zersetzung als auch die indirekten Effekte der Umwelt über den Einfluss auf die Pilzdiversität getestet. Es zeigte sich, dass Baumart und Kronenbedeckung die stärksten Prädiktoren für die Zersetzungsrate waren. Dabei zersetzte sich Buchenholz stärker als Tannenholz, und in offenen Beständen war der Abbau größer als in geschlossenen. Obwohl Umweltfaktoren die Pilzdiversität beeinflussten, war der direkte Einfluss der Pilzdiversität auf die Zersetzung schwach und inkonsistent zwischen den Baumarten und Erhebungsmethoden. Diese Erkenntnisse deuten darauf hin, dass die Zersetzung von Totholz sowie die damit verbundenen Kohlenstoff- und Nährstoffkreisläufe maßgeblich durch klimawandelbedingte Störungen und

forstwirtschaftliche Maßnahmen beeinflusst werden, insbesondere durch Störungen der Baumkronen und die Auswahl der Baumarten.

Zusammenfassend belegen die Ergebnisse, dass Kronenöffnungen maßgeblich die innere Totholztemperatur beeinflussen und die Zersetzungsprozesse beschleunigen können, was langfristig zu einer Reduktion der Kohlenstoffspeicherung und einer verstärkten Kohlenstofffreisetzung führen könnte. Obwohl sich die Pilzgemeinschaften insgesamt als relativ widerstandsfähig erwiesen haben, hängen sowohl deren Vorkommen als auch die Totholzzersetzung stark von der Verfügbarkeit von Feuchtigkeit ab – ein Faktor, der unter zunehmender Dürrehäufigkeit insbesondere in offenen Beständen kritisch werden könnte. Künftige Forschung sollte daher verstärkt die Wechselwirkungen zwischen Feuchtigkeit und Temperatur auf Ebene einzelner Totholzobjekte sowie deren gemeinsame Effekte auf die Diversität und Funktion von Zersetzergemeinschaften berücksichtigen.

SUMMARY

Global climate change affects forest ecosystems directly (e.g., via temperature increase) and indirectly (e.g., via disturbances such as windthrows). These changes affect forest ecosystem structures and processes, including deadwood, which provides critical habitats and supports key ecosystem functions. Deadwood decomposition is essential for regulating carbon and nutrient cycles in forest ecosystems. However, it is influenced by a complex interaction between environmental conditions and wood-decaying organisms. Climate change-induced disturbances, such as windthrows, increase deadwood quantity and heterogeneity when not salvage logged, while altering stand microclimate through canopy loss. These changes can profoundly affect deadwood decomposition and related processes. Among these, microclimate emerges as a critical factor, with previous studies demonstrating its capacity to directly influence decomposition rates and decomposer community composition. Nevertheless, considerable knowledge gaps persist regarding how environmental variables at both the stand and object scales impact the internal deadwood temperature, thus potentially influencing colonization and activity of decomposers, such as deadwood-inhabiting fungi. Although it is well established that microclimatic conditions at the stand scale can shape the diversity of deadwood-inhabiting fungi, the consequences of sustained microclimatic shifts on fungal succession remain largely unknown. Furthermore, the interplay between abiotic factors, fungal diversity, and their combined effects on decomposition dynamics is poorly understood. Most studies have examined environmental parameters or fungal diversity in isolation, often neglecting the direct and indirect effects of the environment on fungal diversity-decomposition relationships. To address these knowledge gaps, I analyzed data from a long-term deadwood experiment established in 2011 in the Bavarian Forest National Park.

In the first part of my dissertation, I examined how stand-scale factors (canopy openness, surrounding deadwood amount) and object-scale factors (tree species, deadwood diameter, deadwood position) affect internal deadwood temperature. Canopy cover emerged as the most important factor influencing deadwood temperature. During the growing season (May-October), daily mean and maximum temperatures of deadwood objects were significantly higher, while daily minimum temperatures were lower, in open canopies compared to closed canopies. In winter (November-April), open canopies resulted in lower daily minimum temperatures. These temperature differences were significant, with annual mean and maximum temperatures in open canopies being approximately 1 °C and 5 °C warmer, respectively, and minimum temperatures being about 2 °C colder, compared to closed canopies. Other factors,

including surrounding deadwood amount, deadwood position (soil contact versus uplifted), deadwood diameter, and tree species, had weaker and less consistent effects on internal deadwood temperature, with statistically significant effects observed in a few months. These results suggest that, under climate change, increasing windthrows could alter internal deadwood temperatures, potentially affecting habitat conditions for deadwood-decomposing organisms and related ecological processes.

Second, I analyzed how canopy-mediated microclimate influences fungal succession, focusing on fungal fruit body diversity and community composition. Over 10 years, fungal diversity initially increased during the early stages of succession and subsequently decreased, with a more pronounced decline under open canopies. Despite these changes in diversity, community dissimilarity between canopy treatments remained largely stable, with approximately 25 % of fungal species exclusive to either open or closed canopies. Species exclusive to open or closed canopies were found on fewer deadwood objects compared to those occurring in both canopy conditions. These results suggest that fungal succession on deadwood is relatively resilient to changes in canopy cover due to species specialization or tolerance.

Third, I investigated factors influencing deadwood decomposition, focusing on how environmental variables and fungal diversity contribute to deadwood density loss after 10 years of decomposition. I addressed the previously mentioned knowledge gap by explicitly testing simultaneously the direct effect of fungal diversity, as well as both the direct environmental effects on density loss and the indirect effects mediated through fungal diversity. My results showed that tree species and canopy cover were the primary drivers of deadwood decomposition. Beech logs showed higher density loss compared to fir logs, and deadwood in open canopies exhibited higher decomposition than in closed canopies. Although environmental factors influenced fungal diversity, the direct effects of fungal diversity on decomposition were weak and inconsistent across tree species and sampling methods. These findings suggest that deadwood decomposition and the associated carbon and nutrient cycles are largely shaped by climate-induced disturbances and forest management practices, particularly canopy disturbance and tree species selection.

In conclusion, my studies demonstrate that canopy openings influence deadwood temperature regulation and accelerate decomposition, potentially reducing carbon sequestration and increasing carbon release. Although fungal communities showed overall resilience, fungal occurrence and deadwood decomposition strongly depend on moisture availability, which may decline with more frequent droughts, particularly under open canopy conditions. To fully

understand the resilience of these communities and the long-term dynamics of deadwood habitats, future research should address key knowledge gaps concerning the interplay of moisture and temperature at the object scale and their combined effects on fungal diversity and decomposition processes.

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Abbreviations	Definition
a.s.l.	Above sea level
BEF	Biodiversity-ecosystem functioning
CWD	Coarse woody debris
FWD	Fine woody debris
MAP	Mean annual precipitation
MAT	Mean annual temperature
OTU	Operational taxonomic unit

1 INTRODUCTION

Forest ecosystems cover approximately 31 % of the global terrestrial land area (FAO, 2020). They provide a wide range of ecosystem services, including climate regulation, carbon sequestration, soil stabilization, water retention, support of biological diversity (Krieger, 2001), and human recreation (Meyer et al., 2019). However, global climate change significantly affects forest ecosystems and ecosystem services at various scales due to increasing atmospheric CO_2 concentrations, which alter mean annual temperatures and precipitation patterns (IPCC, 2023). These alterations challenge the stability of the environmental parameters to which tree species are evolutionarily adapted, as their ecological niches are defined by specific interactions between environmental (e.g., climatic) and biological (e.g., habitat structure, competition) conditions (Pocheville, 2015). They are long-living organisms that are not able to change their location, and it is unlikely that they will be able to track the rapid changes in future climate conditions (Aitken et al., 2008; Corlett and Westcott, 2013). Thus, tree species are especially vulnerable to climate change, potentially leading to maladapted forest ecosystems (Maciver and Wheaton, 2005). Furthermore, current forest management with monocultures and harvested deadwood up to 90 % of the potential deadwood volume due to intensified utilization, pest control, or biofuels further leads to less resilient forest ecosystems naturally (Stokland et al., 2012). This is particularly evident in the fact that forest ecosystems are poorly adapted to the indirect effects of climate change, such as increasing disturbance events such as droughts, windthrows, pest infestations (e.g., bark beetles), and fires (Seidl et al., 2014; Turner, 2010).

These future disturbance events might exceed the range of natural disturbance variability and increase in both frequency and intensity (Millar and Stephenson, 2015; Seidl et al., 2017; Senf et al., 2018), which makes disturbed areas particularly vulnerable to further disturbances due to their low resilience (Buma, 2015; Johnstone et al., 2016; Paine et al., 1998). Thus, recovery of forest canopies to pre-disturbance conditions might exceed several decades. Windthrows are the most prevalent disturbances affecting forest ecosystems in Western and Central Europe (Senf and Seidl, 2021). They increase tree mortality, leading to an accumulation of dead trees, which serve as an essential biological legacy when not salvage-logged for pest control (Bässler et al., 2016). Additionally, windthrows enhance the structural complexity and spatial heterogeneity of forests by contributing deadwood of various diameter classes (logs and branches) and positions (lying or uplifted) (Priewasser et al., 2013; Ruel, 1995; Swanson et al., 2011).

The resulting deadwood is essential for water and nutrient storage, supports soil development, and contributes to the global carbon cycle by storing, exchanging, and regulating carbon dynamics (Forrester et al., 2012; Pichler et al., 2012). Globally, deadwood accounts for approximately 8 % of forest carbon stocks (Pan et al., 2011). As deadwood decomposes, carbon is transferred to forest soils (Błońska et al., 2019), though this process can take years to decades depending on various factors (Hararuk et al., 2020). However, during decomposition, deadwood is a biodiversity hotspot, with approximately 25 % of forest-dwelling species relying on deadwood, either indirectly, through interactions with wood-decomposing organisms at various stages of their life cycles, or directly, as a habitat or food source by feeding on bark, phloem, or wood (Parisi et al., 2018; Siitonen, 2001; Stokland et al., 2012). Those species are defined as saproxylic species (Stokland et al., 2012). The most important wood decomposers are fungi, bacteria, and invertebrates (Begon et al., 2006; Cornwell et al., 2009).

Overall, the decomposition of deadwood is influenced by complex interactions between environmental variables and saproxylic diversity that vary across temporal and spatial scales. Studies have shown that climate (macro- and microclimate), tree species identity, related wood characteristics, and wood-decomposing organisms affect deadwood decomposition (Erdenebileg et al., 2020; Jacobs and Work, 2012; Janisch et al., 2005; Přívětivý et al., 2016; Seibold et al., 2016b; Shorohova and Kapitsa, 2014). However, despite these insights, important knowledge gaps remain. While macroclimate refers to regional climate patterns, forest microclimate describes the local, small-scale conditions within a stand, with canopy cover often used as a proxy. Nevertheless, microclimatic conditions can vary not only at the stand scale but also at the scale of individual objects, and the specific environmental and object-related factors influencing microclimate at this finer scale remain poorly understood. At both the stand and object scales, microclimatic conditions shape the immediate abiotic environment of deadwood, defining the niches and thus the colonization and activity of wood-decomposing organisms. While the influence of stand-scale microclimate on wood-inhabiting fungal communities, which are key deadwood decomposer (Boddy and Watkinson, 1995), is evident (e.g., Krah et al., 2018, further details in Chapter 1.2), its role in driving species succession, an essential process in decomposition, remains poorly understood. Additionally, the roles of environmental factors, wood-inhabiting fungal diversity, and their intricate interdependence in regulating deadwood decomposition has yet to be fully elucidated. To address these gaps, the following introduction will provide a comprehensive overview of current knowledge regarding the effects of disturbances on microclimate and deadwood characteristics, with particular focus on deadwood temperature. It will also summarize existing research on the ecology of wood-

decomposing fungi and the environmental factors influencing deadwood decomposition. This framework aims to identify and clarify the remaining knowledge gaps and guide further investigation.

1.1 Forest microclimate and internal deadwood temperature in a changing climate

In undisturbed forest ecosystems, which are characterized by a three-dimensional canopy structure, the local microclimate is moderated through processes such as evapotranspiration, shading, and air mixing (Zellweger et al., 2020). Intact canopies buffer macroclimate conditions, leading to more stable climatic conditions within forest stands. This effect depends on factors such as stand structure (e.g., tree species, age) and mortality events (Thom et al., 2020; Zellweger et al., 2020). Although the buffering capacity of canopy cover is influenced by temporal fluctuations in macroclimatic conditions as well as local stand and site characteristics (Rita et al., 2021; Thom et al., 2020), the buffering effect functions in both directions: during winter, temperatures under an intact forest canopy are higher, while in summer, temperatures are lower compared to the macroclimate. This buffering effect can range from 1 °C up to 7 °C (De Frenne et al., 2019; Zellweger et al., 2024). However, canopy loss due to disturbances (e.g., windthrows, forest management) directly influences the local microclimate by reducing the buffering capacity and leading to more open canopies (Schmidt et al., 2017). Canopy openings are generally characterized by increased sunlight penetration, reduced moisture contents, and greater temperature fluctuations, with lower minimum and higher maximum temperatures across both daily and annual cycles (De Frenne et al., 2021; Magnago et al., 2015; Thom et al., 2020; Zellweger et al., 2020).

Since temperature is one of the most critical predictors of biological processes (Clarke, 2017), understanding the factors at both stand- and object-scale that influence internal deadwood temperatures is essential. Studies focusing on internal deadwood temperature across years are scarce. Recent studies have shown that internal deadwood temperatures are higher in open canopies compared to closed canopies (Lindman et al., 2022; Romo et al., 2019). For instance, in pine deadwood, the average maximum temperature during summer months was approximately 5-6 °C higher in open canopies than within pine stands (Romo et al., 2019). More broadly, climate change not only directly increases temperatures but also indirectly intensifies canopy disturbances, which reduce the microclimatic buffering capacity of the canopy and increase canopy openness. A crucial first step in understanding the implications for deadwood and, consequently, ecosystem processes is to analyze the internal deadwood temperatures under varying canopy conditions. Furthermore, the accumulation of deadwood

from disturbances may additionally influence the internal temperature of deadwood objects through increased thermal absorption, as their low albedo enhances heat retention (Cherubini et al., 2012). For instance, snowmelt studies have shown that deadwood increases local temperatures, capturing more radiation potentially due to the black body effect (Štícha et al., 2010), accelerating snowmelt rates (Marangon et al., 2022). Cherubini et al. (2012) also proposed that albedo increases with the removal of organic material from forest ecosystems. However, other studies at the stand scale have found no notable effect of deadwood on forest microclimate (Kovács et al., 2017; Thom et al., 2020), but it remains uncertain whether surrounding deadwood influences the internal temperature of deadwood.

At the scale of an individual deadwood object, the internal temperature may be influenced by several factors. The diameter of the objects influences internal deadwood temperature, with the internal average minimum temperature of logs increasing from the surface to the center, while temperature variability decreases with depth (Romo et al., 2019; Walczyńska and Kapusta, 2017). Thus, deadwood temperature stabilizes with increasing diameter (Pouska et al., 2016). However, the influence of diameter on deadwood temperature remains unclear when considering other confounding factors, such as the position of deadwood objects. Deadwood can occur in various positions within forest stands, such as standing snags, uplifted logs (e.g., with a root plate), or lying branches and logs (Swanson et al., 2011). Standing deadwood tends to be warmer than downed wood due to greater solar exposure (Hutchison and Matt, 1977; Lindman et al., 2022). In addition, increased soil contact in downed deadwood can increase moisture content (Jaroszewicz et al., 2021), potentially cause localized cooling (Pouska et al., 2016). Furthermore, differences in decay stages between standing and downed deadwood may also affect water retention and temperature regulation of deadwood objects (Uhl et al., 2022). Thus, the degree of soil contact of a deadwood object may play a crucial role in shaping its internal temperature dynamics. Beyond external characteristics such as diameter and position, species-specific physical and chemical properties inherent to the deadwood (Lombardi et al., 2013; Pietsch et al., 2014; Weedon et al., 2009) may also influence internal temperature by affecting heat retention and thermal conductivity. This raises the question of whether tree species with varying physico-chemical characteristics exhibit different internal temperatures under similar environmental conditions. This dissertation aims to address the knowledge gap regarding internal deadwood temperature by analyzing the contribution of individual environmental and object-scale factors within the complex hierarchy of scales that influence deadwood temperature, which may, in turn, affect the occurrence of key decomposer species.

1.2 Effect of different microclimatic conditions on wood-inhabiting fungal diversity patterns

Wood-inhabiting fungi are key decomposers of deadwood (Boddy and Watkinson, 1995). They are organisms with a modular structure, characterized by mycelium, a complex network of hyphae, which grows in and is specifically adapted for the efficient exploitation of the substrate (deadwood) (Baldrian, 2017; Nagy et al., 2017). Many species produce multicellular fruiting bodies, which serve as the basis for spore production in sexual reproduction (Nagy et al., 2017). Before producing fruiting bodies, the mycelium must reach a critical size (e.g., biomass), and species that successfully grow as mycelium and form fruiting bodies must endure environmental conditions both within and above the substrate (Krah et al., 2021; Kües and Liu, 2000; Luo et al., 2021). For example, fungi exhibit higher enzymatic activity as temperatures increase, but only up to a critical threshold where protein denaturation begins (Boddy et al., 2014). Similarly, the moisture content of the substrate plays a crucial role in fungal fruiting body growth, with constrained moisture levels, whether too low or too high, negatively affecting growth (Boddy et al., 2014). Thus, wood-inhabiting fungi are ectotherms, i.e., organisms regulating their body temperature primarily through external thermal conditions. Consequently, microclimate defines the thermal niche of wood-inhabiting fungi, influencing their community composition (Lennon et al., 2012; Maynard et al., 2019) and their metabolic rates, which is the rate at which an organism converts chemical energy stored in food sources into usable energy, including enzymatic activity related to wood decomposition (Magan, 2008). Thus, changes in forest microclimate directly influence wood-inhabiting fungal diversity (Krah et al., 2018; Lindhe et al., 2004; Müller et al., 2020; Vogel et al., 2020).

Krah et al. (2018) found in a real-world experiment that the richness of wood-inhabiting fungi was slightly higher, though not significantly, under closed canopies compared to open canopies. Additionally, the fungal composition differed significantly between closed and open canopies for deadwood of two tree species in this study (Krah et al., 2018). Although, fungal diversity is influenced by environmental conditions which shift with both decomposition and time, our understanding of the succession of wood-inhabiting fungal species, both in general and under contrasting microclimate and thus canopy conditions, remains limited. Recent studies mainly focused on the early years and stages of decay (Krah et al., 2018; Lindner et al., 2011), did not explicitly analyze fungal succession (Perreault et al., 2023), focused on a subset of fungal taxa (Norberg et al., 2019), or surveyed different decay stages across separate deadwood objects rather than tracking succession on the same objects (Hart et al., 2024; Holec et al., 2020; Holec

and Kučera, 2020; Jomura et al., 2022; Lepinay et al., 2021). Thus, the effects of permanent microclimate changes in forest ecosystems on the succession of wood-inhabiting fungal species on deadwood remain largely unknown. Studies that have investigated fungal succession found species diversity peaking at intermediate decay stages based on fruit body data and at later decay stages based on data detected via eDNA barcoding methods (hereafter metabarcoding) (Kielak et al., 2016; Ovaskainen et al., 2013). Species succession is influenced by the species composition of the initial colonizers, endophytic fungi in living trees (Parfitt et al., 2010), and opportunistic species (Boddy, 2001), causing priority effects. Since wood-inhabiting fungal species undergo succession during deadwood decomposition (Lepinay et al., 2021), and moisture and temperature are critical factors influencing fungal growth (Boddy and Heilmann-Clausen, 2008; Brabcová et al., 2022), differences in microclimate can be expected to affect species richness and community composition across successional stages. For example, if species that colonize at different time points vary in their tolerance to warmer temperatures, this could lead to a decline in species that are less heat-tolerant due to physiological constraints. Thus, differences in the successional patterns of wood-inhabiting fungal species diversity may potentially impact ecosystem processes such as decomposition (Barbé et al., 2020; Maynard et al., 2019). Analyzing the effect of closed and open canopies on fruiting species richness and community composition helps clarify how disturbances that create open canopies influence fungal species succession. This, in turn, can indicate how disturbances affect subsequent changes in decomposition processes.

1.3 Complex relationship between fungal diversity and environmental factors influencing deadwood decomposition rates

In general, deadwood decomposition involves a complex interaction between environmental conditions and wood-inhabiting fungal diversity. On a stand-scale, microclimatic conditions are the main factor defining deadwood decomposition rates. Deadwood decomposes faster under open canopies than under closed canopies (Janisch et al., 2005; Shorohova and Kapitsa, 2014), likely due to mechanisms such as photodegradation (George et al., 2005; Li et al., 2016), physical stress (e.g., cracks), leaching, and weathering (Fravolini et al., 2018; Harmon et al., 1986; Russell et al., 2015; Zhou et al., 2007). Furthermore, disturbance legacies such as higher amounts of surrounding deadwood may directly influence decomposition rates by potentially modifying microclimatic conditions (see Chapter 1.1). The species-energy theory may further explain the potential effects of deadwood amount in the surroundings on decomposition through species diversity. It suggests that an increase in available chemical energy and habitat area

(deadwood volumes) leads to higher individual numbers and higher species diversity (Schuler et al., 2015; Srivastava and Lawton, 1998; Wright, 1983). Additionally, the deadwood heterogeneity in the surroundings, such as variations in the composition of different tree species and deadwood sizes (such as fine woody debris (FWD) and coarse woody debris (CWD)), may also indirectly influence decomposition processes. According to the habitat heterogeneity hypothesis, a greater variety of habitats can promote higher species diversity (MacArthur and MacArthur, 1961). Thus, deadwood heterogeneity may positively influence the abundance and diversity of saproxylic species (Seibold et al., 2016b). Therefore, an increased amount of surrounding deadwood and greater structural diversity may influence decomposition rates by promoting decomposer diversity.

At the object scale, deadwood decomposition is influenced by tree species identity, with angiosperm wood tending to decompose more rapidly than gymnosperm wood (Herrmann et al., 2015; Kipping et al., 2022; Weedon et al., 2009), primarily due to species-specific differences in chemical and morphological traits (Kahl et al., 2017). Traits such as higher nitrogen and phosphorus content, which are more common in angiosperms, enhance decomposition, whereas higher concentrations of lignin and phenols, typical of gymnosperms, tend to inhibit it (Kahl et al., 2017; Weedon et al., 2009). These differences are most pronounced during the early stages of decomposition and tend to diminish over time (Oberle et al., 2020). However, the relative importance of tree species compared to other environmental factors on deadwood density loss remains unclear.

The actual breakdown of wood components is largely mediated by the activity of wood-inhabiting fungi. Wood-inhabiting fungi often exhibit strong host specificity, with certain species restricted to either gymnosperms or angiosperms, and generalist species occurring on both (Müller et al., 2020; Purahong et al., 2018). However, wood-inhabiting fungi are the most efficient decomposers in temperate and boreal forests (Gómez-Brandón et al., 2020; Perreault et al., 2023), utilizing a wide array of extracellular enzymes (e.g., ligninolytic enzymes, Arnstadt et al. (2016)) and using other non-enzymatic strategies (e.g., hydroxyl radicals) to degrade all wood components (Goodell et al., 2017). However, the relationship between the diversity of wood-decaying fungi and decomposition is not straightforward. Some studies have found positive effects between the number of fungal species and decomposition, suggesting facilitative interactions such as niche complementary (e.g., Kahl et al. (2015); Lustenhouwer et al. (2020)), while others have reported negative effects, indicating antagonistic interactions such as competition (Fukami et al. (2010); Leonhardt et al. (2019); Perreault et al. (2023); Fukasawa and Matsukura (2021)). Recent research suggests that community composition might be a more

reliable predictor than species richness (Hoppe et al., 2016; Pietsch et al., 2019; Yang et al., 2024). Additionally, the prevalence of dominant species provides a better explanation for deadwood decomposition than diversity measures that treat all species equally (Kipping et al., 2024). Consequently, incorporating advanced diversity metrics that account for species abundance, such as Hill numbers, could provide deeper insights into the relationship between fungal diversity and decomposition processes (Chao et al., 2016). However, the relationship between fungal diversity and decomposition rates is complex, and a recent study emphasized that inconsistencies in the fungal-decomposition relationship among real-world studies might be caused by an ignorance of environmental factors that affect deadwood decomposition directly and indirectly via diversity (Runnel et al., 2024). Therefore, studies simultaneously assessing the direct effects of environmental factors and the indirect effects mediated by wood-inhabiting fungal diversity on deadwood decomposition are still lacking.

2 OBJECTIVES

The overarching objective of this dissertation is to gain an in-depth understanding of the effects of changing environmental conditions on deadwood processes and their interaction with associated wood-inhabiting fungal diversity. Central to this work is the role of forest stand-scale microclimate variation, particularly contrasting closed versus open canopy cover, as a driver of biotic and abiotic processes within deadwood. It aims to provide knowledge needed to support the development of recommendations for deadwood management in forests in the context of climate change, aiming to preserve key ecosystem services, such as carbon sequestration during deadwood decomposition, related abiotic and biotic processes, and saproxylic species diversity. To achieve this, an experimental approach was employed using data from a large-scale real-world experiment in the Bavarian Forest National Park. The research specifically concentrates on the following three objects:

In a first step, I investigated how stand-scale environmental variables (canopy cover, amount of deadwood in the immediate surroundings) and object-scale characteristics (tree species identity, object position, and object diameter) influence internal temperature within deadwood logs (Figure 1, Objective 1). This analysis aims to disentangle the contributions of these hierarchical factors on the daily mean, minimum, and maximum temperatures of deadwood at both monthly and seasonal scales. The results may provide a foundation for future research on how climate change-induced changes at the stand- or object-scale affect internal deadwood temperature, potentially leading to shifts in deadwood-dwelling species and ecological processes.

In the second part, I examine how different microclimates (closed vs. open canopy cover) affect the succession of fungal species on standardized deadwood objects (CWD and FWD) beyond the initial years and stages of decay (Figure 1, Objective 2). For this purpose, I calculated the treatment-based alpha and beta diversity, utilizing the Hill framework, which allows the incorporation of species incidence and abundances in a unique approach, and thus emphasizes the diversity of rare, common and dominant species (further explanations see Chapter 3.2.2). This complements the first part of this dissertation by linking forest stand microclimate to long-term patterns in wood-inhabiting fungal diversity and provides a more comprehensive understanding of how fungal species perform under different microclimatic conditions during succession.

Finally, the environmental stand-scale variables from Objective 1 (canopy cover, amount of deadwood in the immediate surroundings) were augmented by the heterogeneity of deadwood

in the immediate surroundings and fungal alpha and beta diversity (based on fruit body and metabarcoding data), to test the direct (environment and decomposer diversity) and indirect effects (environment via decomposer diversity) simultaneously on the decomposition of deadwood logs. I used deadwood density loss as a proxy for deadwood decomposition. Similar to Objective 2, and to increase inferences, I applied the Hill framework to test diversity effects while accounting for species abundance (Figure 1, Objective 3). The results offer a deeper understanding of deadwood decomposition rates by unraveling the complex interactions between stand-scale factors and wood-inhabiting fungal diversity that influence decomposition.

The following research questions are guiding this dissertation:

I) How do stand- and object-scale factors affect internal temperature dynamics in deadwood, and do their contributions differ between monthly and seasonal scales?

II) How do contrasting microclimatic conditions affect wood-inhabiting fungi's successional trajectory and diversity patterns on deadwood?

III) How do stand-scale environmental factors and wood-inhabiting fungal diversity directly and environmental factors indirectly affect deadwood density loss via fungal diversity?

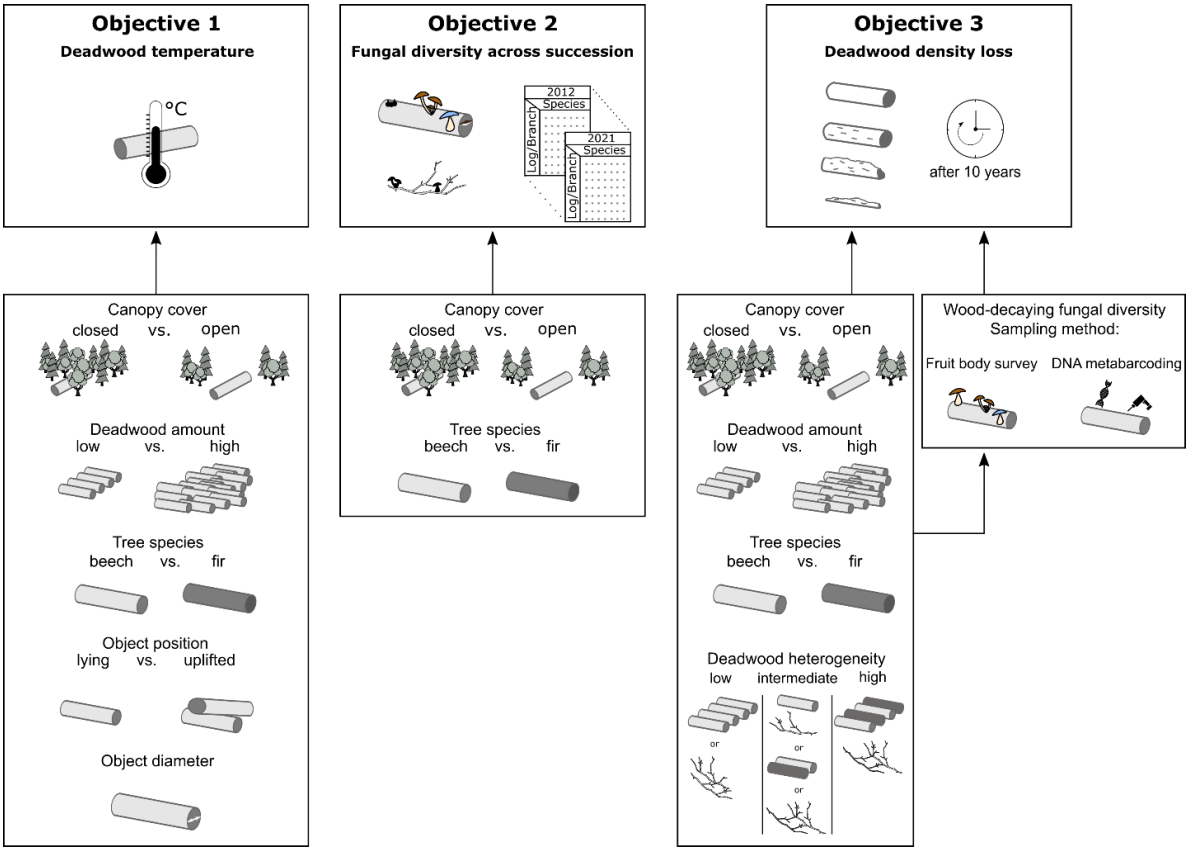

Figure 1: Concept figure of the three objectives of this dissertation. The first study addresses the effect of different stand-scale (canopy cover, deadwood amount in the surrounding) and object-scale (tree species, object position, object diameter) variables on within-deadwood temperatures (mean, minimum, and maximum) to achieve ***Objective 1****. The second study addresses the succession of wood-decaying fungal fruit body diversity on deadwood logs and branches from two tree species under both closed and open canopy conditions over 10 consecutive years, aiming to achieve* ***Objective 2****. The third study addresses the direct effects of the environment and fungal diversity, and indirect effects (environment via wood-inhabiting fungal diversity) on deadwood decomposition (using density loss as a proxy) after 10 years of deadwood succession to achieve* ***Objective 3****.*

3 MATERIALS AND METHODS

The three research questions of this dissertation could be investigated using a real-world deadwood experiment in the Bavarian Forest National Park, in southeastern Germany, which was established in 2011. Within this experiment, I can simultaneously investigate the effects of possible future environmental conditions in forest stands on deadwood processes and wood-inhabiting fungal diversity. Due to the manipulation of environmental conditions, the experimental approach gives more reliable results on the interaction between environmental conditions, deadwood processes, and wood-inhabiting fungal diversity compared to field surveys. The following section gives a brief overview of the Bavarian Forest National Park and the experimental setup.

3.1 Study area

3.1.1 Bavarian Forest National Park

The Bavarian Forest is a mountain range, located in southeastern Germany (48°54'N, 13°29'E), which became partly a national park in 1970 with a current size of ca. 24,000 hectares at elevations from 650 to 1450 m a.s.l. (Bässler 2004). Climate conditions vary with altitude, with mean annual temperature (MAT), ranging from 3.5 °C to 7.0 °C (1972-2001), and the mean annual precipitation (MAP), ranging from 1,300 to 1,900 mm per year (Bässler, 2004). The growing season in the Bavarian Forest with the highest species activity, including deadwood-dependent species of beetles and fungi, spans roughly between May and October (Bässler et al., 2015; Krah et al., 2018; Lettenmaier et al., 2022; Seibold et al., 2016a). In elevations lower than 1,100 m, mixed montane forests dominated by Norway spruce (*Picea abies* (L.) H. Karst), European beech (*Fagus sylvatica* L.), and Silver fir (*Abies alba* Mill.) occur. In higher elevations (> 1,100 m), the high mountain forests are dominated by spruce and a lower amount of beech and Mountain Ash (*Sorbus aucuparia* L.) (Bässler et al., 2010). The amount of deadwood in the core zone of the national park increased to more than 700 m^3/ha due to disturbance events such as windthrows and bark beetle infestations, combined with a prohibition on salvage logging in the core zone (Bässler et al., 2010; Müller et al., 2008).

3.1.2 Large-scale deadwood experiment

In 2011, a large-scale deadwood experiment was conducted in the management zone of the Bavarian Forest National Park. The description of the experiment is based on the description of Krah et al. (2018) and Seibold et al. (2016b). The experiment was established on 180 plots with a size of 0.1 ha arranged in a random block design in five different sites (blocks) across the

management zone. Deadwood was harvested using chainsaws from stands with similar conditions (e.g., elevation, age, tree species composition). Overall, ca. 7,400 deadwood objects of four different types were deposited: logs (CWD, diameter: 20-50 cm, length: 5 m) and branches (FWD, diameter: 3-5 cm, length: 2-3 m) of beech and fir. Each plot contains either FWD or CWD, or a combination of both, and either beech or fir, or both (Seibold et al., 2016b), establishing three levels of deadwood heterogeneity: low, medium, and high. The lowest heterogeneity included one of four substrate types (fir FWD, fir CWD, beech FWD, or beech CWD). Intermediate heterogeneity included one tree species with both diameter classes (fir CWD and fir FWD or beech CWD and beech FWD) or both tree species with one diameter class (fir and beech CWD or fir and beech FWD). The highest heterogeneity included both tree species and both diameter classes. The calculated deadwood heterogeneity index is based on Siitonen et al. (2000) and applied in several studies (e.g., Seibold et al., 2016b). Half of the plots had a low volume of deadwood (8 branches of ca. 0.2 m^3/ha or 4 logs amounting to approximately 10 m^3/ha), while the other half had a high volume of deadwood (80 branches of ca. 2 m^3/ha or 40 logs of ca. 100 m^3/ha). In each site, each combination of deadwood heterogeneity and amount was created twice. Half of the plots (19) were established under closed canopies, while the other half were placed under open canopies, as canopy cover serves as a proxy for microclimate (Vodka et al., 2009). The open canopies resulted from clearings where all living and dead trees were removed, and annual mowing maintained the openness of the plots. Previous studies showed significant temperature differences on deadwood surfaces between open and closed canopies within the same experiment (Krah et al., 2022; Müller et al., 2020). In August 2018, they measured the surface temperatures of 136 logs using an infrared thermal sensor, finding notable differences in LiDAR penetration rate and temperature between the canopy types, indicating varying radiation availability near the ground (Müller and Vierling, 2014).

3.2 Data sampling, preparation, and statistical analyses

To achieve the objectives of the thesis, various data were measured and/or sampled within the large-scale deadwood experiment. The following provides an overview of the sampling methods and the statistical analyses. All data preparation and statistical analyses were conducted using R 4.3.0 (R Core Team, 2023). For a more detailed description, please refer to the method sections in the manuscripts (Manuscripts 10.1, 10.2, 10.4).

3.2.1 Objective I: How do stand- and object-scale factors affect internal temperature dynamics in deadwood, and do their contributions differ between monthly and seasonal scales?

3.2.1.1 Study design and data sampling

In twelve plots of the large-scale deadwood experiment, located in four of the five sites, the internal deadwood temperature was measured in a total of 50 logs. Half of the plots were in closed canopies, and the other half were in open canopies. The selected plots contained either low amounts of surrounding deadwood (25.20 m^3/ha on average) or high amounts (178.12 m^3/ha on average). Three to five beech and/or fir deadwood objects (logs (CWD), diameter: 19-47 cm, mean: 32 cm, length: 5 m) in various positions were randomly selected on each plot to balance the number of objects across the plots. These logs were either lying on the ground or uplifted, stacked over other logs with less than 50 % soil contact. In total, the experiment included 26 logs in open canopies and 24 logs in closed canopies, comprising 25 beech and 25 fir logs. Of these, 23 were elevated and 27 had complete soil contact.

Temperature measurements, inside the wood sub-surface layer of the 50 deadwood objects, were conducted in a 15-minute interval by colleagues (see Chapter 8) from May 19th, 2016, to October 31st, 2019, using Pt100 resistance thermometers connected to data loggers (MINILOG-T6, Fiedler AMS, České Budějovice, Czech Republic). Each log had one thermometer placed in the cross-section (in uplifted logs, the uplifted cross-section was used), positioned 5 cm below the surface and 10 cm deep inside the log. In uplifted logs, thermometers were inserted into the upper ends, and at each measuring point, the log diameter was measured. This approach allowed for comparison with other studies, and temperature measurements at this depth have been shown to significantly correlate with saproxylic diversity (Pouska et al., 2016; Pouska et al., 2017).

3.2.1.2 Data preparation

First, I harmonized temperature data for the three years and cleaned it from potentially unrealistic values, which I compared with temperature data from a nearby meteorological station (Waldhäuser). Second, I calculated the daily mean, minimum, and maximum temperatures from the cleaned 15-minute values. Furthermore, based on these data, I identified thermometers, which were most likely covered with snow during wintertime based on temperature thresholds, with daily maximum and daily minimum temperatures remaining constant or not exceeding certain thresholds, which were adapted from the ‘myClim’ package in R (Man et al., 2023). I removed detected snow days when the Waldhäuser and Großer Rachel meteorological stations also recorded snow on the respective date. In all years, January

consistently had a high number of snow days, therefore, I omitted January from the analysis. Due to this procedure and the temporary failure of some data loggers, I could use the data from June-December in 2016, February-November in 2017, February-December in 2018, and March-October in 2019.

3.2.1.3 Statistical analysis

I applied multivariate linear mixed-effect models (*lme* function within the R package 'nlme' (Pinheiro and Bates, 2000)) to test simultaneously the influence of stand-scale variables (canopy cover, surrounding deadwood amount) and object variables (diameter, position, tree species) on the mean, minimum and maximum temperature inside deadwood based on daily data, both on monthly and season level. Seasons were defined i) biologically, based on biodiversity survey data, as the period with the most species activity (May-October, see Section 3.1.1), and winter time (November-April), and ii) meteorologically: spring (March-May), summer (June-August), autumn (September-November), and winter (December-February) (Deutscher Wetterdienst, 2024), to enable comparison with similar studies. In addition to the explanatory variables (canopy cover, surrounding deadwood amount, object diameter, object position, tree species), I included the mean annual temperature of the respective years (2016-2019) from the nearby meteorological station Waldhäuser as a covariate. Canopy cover (open vs. closed), surrounding deadwood amount (high vs. low), position (lying vs. uplifted), and tree species (beech vs. fir) were initially included as factorial predictors. Since the deadwood amount (m^3/ha) was measured for each plot and showed high variability within the high and low categories, I treated the deadwood amount as a continuous variable. However, it is important to note that the results of the analysis remained robust when the deadwood amount was treated as a factorial predictor. As a result, the final continuous predictors used in the models were deadwood amount and log diameter, which were standardized using z-transformations. All response variables followed a normal distribution, and collinearity among the predictors was low ($r < |0.04|$). I included 'plot within site' as a random effect to account for the nested study design. Additionally, first-order autocorrelation was addressed using the *corAR1* function within the R package 'nlme' to account for potential temporal autocorrelation in consecutive temperature measurements within the linear mixed-effects models. I used the Durbin-Watson statistics (*DurbinWatsonTest* within the R package 'DescTools' (Signorell et al., 2021)) to validate how the autocorrelation term within the models reduces the temporal autocorrelation. For interpreting the results, I used descriptive plots based on the raw values (see supplementary materials of Manuscripts 10.1) and the full model output. I reported the t-values (calculated as the predictor estimate divided by its standard deviation, representing a

type of signal-to-noise ratio) to allow for a direct comparison of the effects among predictors while accounting for data variability. Additionally, I derived the marginal R^2, representing the variance explained by the fixed effects, using the *r.squaredGLMM* function from the 'MuMIn' R package (Barton, 2024).

The Durbin-Watson statistic still indicated a weak temporal autocorrelation (Draper and Smith, 1998; Durbin and Watson, 1950). In response, I used additional models with monthly aggregated mean temperature values as the response variable, following the "5/3 rule" for data completeness suggested by the World Meteorological Organization (Anderson and Gough, 2018). This rule ensured no more than five missing daily values or three consecutive missing daily values within a month (World Meteorological Organization, 2017). I calculated monthly averages of daily mean, minimum, and maximum temperatures of each log, and monthly linear mixed effect models were applied using the *lmer* function in the R package 'lme4' (Bates et al., 2015), with annual temperature in the offset argument to account for the annual difference in mean, minimum and maximum temperature and plot nested within site as a random effect. These models confirmed the robustness of the daily models' inferences with weak temporal autocorrelation. However, I report the results from both modeling approaches to reduce potential bias in interpreting the model with daily resolution. While my monthly data span multiple years, I did not have complete data for every month in each year. Although I included the mean annual temperature for the respective years in the overall models, this variation in data availability could still introduce bias. Addressing this, I also modeled each month of each year separately, based on the available data, which confirmed the results of the overall models. Consequently, I reported the models for each month and season based on all available data across the years.

3.2.2 Objective II: How do contrasting microclimatic conditions affect wood-inhabiting fungi's successional trajectory and diversity patterns on deadwood?

3.2.2.1 Study design and data sampling

For this study, I used fruit body data from 36 plots of the large-scale deadwood experiment, replicated in 5 sites (blocks) across the study area. Half of the plots were under closed canopies (18) and the other half under open canopies (18). Within the 18 plots, various combinations of deadwood tree species and types (CWD and FWD) were used to capture deadwood heterogeneity. Across all plots and canopy treatments, a total of 240 logs (5 blocks * 2 tree species * 24 logs) and 480 branches (5 blocks * 2 tree species * 48 branches) were placed on

the forest floor. Seven deadwood objects were excluded from analysis due to the loss of the objects (branches) or because their labels could not be found (stolen or broken off).

3.2.2.2 Fruit body inventories

Fungal fruit body inventories were conducted every autumn (September/October, the main season of fruit body development (Halme and Kotiaho, 2012)) by observing visible fruit bodies on deadwood. I used fruit body data from all years of the experiment (2012-2021) and both deadwood types (logs and branches). Logs were divided into seven segments for effective and non-redundant sampling, 5 segments on the log surface and two segments at the cut edges. During sampling, branches were treated as a single segment, whereas logs were divided into seven segments to prevent redundant sampling. Fruit bodies were identified in the field or the laboratory by mycological professionals, with voucher specimens deposited in the herbarium of the Bavarian Forest National Park. Nomenclature followed MycoBank (Crous et al., 2004). Additionally, decomposition stages for each segment were estimated in four categories following Albrecht (1990), and the average decay stage per log was calculated. After 10 years, logs and branches were found in various stages of decay, with some beginning to disintegrate.

3.2.2.3 Data preparation

First, I calculated fungal alpha and beta diversity using incidence-frequency, which is defined by the number of dead wood objects occupied by a species. This measure was computed for each canopy treatment and combinations of tree species and deadwood size, both across sites and for each site separately. Despite some limitations in data for individual sites, consistent patterns emerged, leading me to present results across all sites.

In this study, I used the Hill numbers approach, which is widely used in community ecology research (Ellison, 2010; Hill, 1973). Hill numbers calculate diversity as ‘effective number of equally abundant species’, allowing to varyingly emphasize species abundances via an exponent q, on a unified scale, increasing interpretability (Chao et al., 2014b). Specifically, I used the Hill number of order q=0, which corresponds to species presence/absence and emphasizes rare species with low frequencies, reflecting species richness. The Hill number of order q=1 corresponds to exponential Shannon diversity, representing the effective number of common species, while the Hill number of order q=2 corresponds to inverse Simpson diversity, representing the effective number of dominant species. I estimated the alpha diversity of fungal fruiting communities using the *iNEXT* function in the R package 'iNEXT' (Hsieh et al., 2016), which provides diversity estimates based on rarefaction and extrapolation using incidence frequency.

The Hill number framework can also be applied to analyze community composition and beta diversity (Chao et al., 2014a). Thus for beta diversity, I analyzed community dissimilarities using species similarity indices between open and closed canopies for each tree species and year with the *SimilarityPair* function within the R package 'SpadeR' (Chao et al., 2016). The calculated Chao-Sørensen index (q=0) assigns equal weight to all species, emphasizing rare ones. The abundance-based Horn index (q=1) assigns more weight to common species based on their abundance. Lastly, the abundance-based Morisita-Horn index (q=2) is sensitive to dominant species and minimizes the influence of rare species (Chiu and Chao, 2014). I calculated similarities using theses indices and then converted these to dissimilarity values (1-estimated similarity values, ranging from 0 for equal communities to 1 for completely different communities). Each estimate included a 95 % confidence interval based on 100 bootstraps.

3.2.2.4 Statistical analysis

First, I conducted generalized additive models (GAMs) using the function *gam* within the R package 'mgcv' (Wood, 2015), to test how alpha diversity responded to closed and open canopies over time. This approach captures potential non-linear responses, which may be expected due to species accumulation. I did not include interactions between canopy and tree species, treating tree species as study replicates. I also fitted linear models (LMs), using the function *lm* within the R package 'stats' for comparison.

First, I modeled alpha diversity as the response variable, with canopy openness and time (years) as predictor variables, using fewer knots (k=3) than the default in GAMs due to convergence issues. A second GAM included an interaction term between time and canopy treatment to detect divergent patterns over time. Both models were repeated for each tree species, wood size, and Hill number (q). A significant interaction indicated differing slopes between closed and open canopies over time. I also interpreted non-overlapping 95 % confidence intervals to identify trends of differences between canopy treatments each year, while interpreting trends cautiously due to potential non-significance. Linear models were used to test interaction terms more robustly. I fitted models with canopy treatment as a factor and time as a continuous predictor, adding the interaction term in a second model. Both GAM and LM analyses showed no signs of temporal autocorrelation. I focused on the p-values for the interaction term to determine the marginal effect of the canopy-time interaction.

Second, to test if dissimilarity between treatments changed over time, I used GAMs with dissimilarity as the response variable and time as the predictor variable, adding the Hill series q as a grouping factor. This analysis was repeated for each tree species and deadwood type (logs

and branches). I interpreted the overall dissimilarity range of the slope as the dissimilarity between open and closed canopies, with values < 0.5 indicating low dissimilarity. I also calculated a linear model and a posthoc test using the function *TukeyHSD* within the R package 'stats' to compare pairwise dissimilarity means for rare, common, and dominant species, applying Bonferroni corrections where necessary on the interpretation of p-values, by considering significant only those with p-values < 0.016 due to multiple testing along the Hill series with three levels (i.e., 0.05/3).

3.2.3 Objective III: How do stand-scale environmental factors and wood-inhabiting fungal diversity directly and environmental factors indirectly affect deadwood density loss via fungal diversity?

3.2.3.1 Study design and data sampling

For this study, thirty-six plots of the large-scale deadwood experiment in the Bavarian Forest National Park were selected in four sites, across the study area (ca. 48 km², minimum distance between sites: 2.4 km), with half under closed and half under open canopies. Each plot had either one beech or fir log, with six plots containing both. A gradient of surrounding deadwood heterogeneity was created using combinations of tree species (beech and fir) and substrate types (CWD and FWD) (see Section 3.1.2). The plots contained an overall high amount of FWD and CWD (on average: 165.87 m³) with considerable ranges from 103.37 m³ to 231.35 m³. Although the amount of deadwood was not fully standardized across my study plots, it was included as a predictor. Deadwood amount was evenly distributed across the plots and showed no correlation with other predictors.

3.2.3.2 Log disc sampling and wood density measuring

On each plot, I randomly selected one deadwood log, either beech or fir. On six plots, I selected two logs (one beech and one fir), resulting in a total of 42 logs across all plots. In total, I selected 21 logs in open canopies (11 beech, 10 fir) and 21 logs in closed canopies (10 beech, 11 fir). For each of the 42 logs, the first 10 cm of the 5-meter length was cut off on one side using a chainsaw, followed by cutting a log disk approximately 5 cm thick. In the laboratory, the log disks were dried in a drying oven (Memmert U40) at 65 °C until constant weight. For volume and density measurements, each log disk was divided into four sectors, and cylindrical samples were extracted from each sector using a 40 mm diameter hole saw drill. The number of samples per sector depended on the decay heterogeneity and disk diameter to ensure representative sampling of decay characteristics. Typically, two subsamples were taken per sector, resulting

in eight samples per disk. An increase in the number of subsamples did not significantly affect the density loss estimates.

Each sub-sample was first weighed to determine its dry weight. Then, wrapped in a standardized amount (8 cm²) of Parafilm®, its volume was measured using the "volume displacement method". The density (ρ) was calculated by dividing the dry weight (m) by the volume (V) ($\rho = m/V$). The average density of the sub-samples was calculated for each log disk, and the percentage of density loss was determined using the following formula:

$$density\ loss = 100 - \frac{\bar{\rho}}{t_0\ density} * 100$$

Where '$\bar{\rho}$' is the average density of the log disks and 't_0 density' refers to literature values of the dry density of freshly cut logs (0.68 g/ml for beech and 0.41 g/ml for fir, as reported by Lohmann (1987). Finally, the density loss was calculated for each log disk.

3.2.3.3 Fruit body inventories and fungal DNA sampling for metabarcoding

Fungal fruit body inventories were conducted as described in Section 3.2.2.1. However, in this study, I used fruit body data from the experiment from the years 2012, 2013, 2015, 2018, and 2021 and only data from deadwood logs.

Deadwood intended for next-generation sequencing analysis of the fungal community was sampled using a cordless drill in the same years as the fruit body inventory (2012, 2013, 2015, 2018, and 2021). After removing the bark at the drilling points, a sterilized auger was used to collect wood dust from four segments along the entire length of the same log. The dust was then combined into a single composite sample and stored in a sterile plastic bag. Samples were frozen and homogenized into fine powder in the laboratory using liquid nitrogen and a swinging mill (Retsch, Haan, Germany). Total fungal genomic DNA was extracted using the NucleoSpin Soil Kit (Macherey-Nagel, Germany) (see details: Baldrian et al., 2016; Brabcová et al., 2022). PCR amplification of the fungal ITS2 region was performed for microbial community analysis using barcoded gITS7 and ITS4 primers (Ihrmark et al., 2012). Amplicon libraries were prepared with the TruSeq DNA PCR-Free Kit (Illumina) and sequenced on the Illumina MiSeq (2 × 250-base reads) (see details: Brabcová et al., 2022).

Amplicon sequencing data were processed using SEED 2.1.1 (Větrovský et al., 2019). Paired-end reads were merged (Aronesty, 2013), the ITS2 region was extracted (Bengtsson-Palme et al., 2013), and Chimeric sequences were detected and deleted (Edgar, 2010). Sequences were clustered using UPARSE implemented within Usearch (Edgar, 2013) at a 97 % similarity level,

and the most abundant sequences were identified using BLASTn against UNITE 9 (Nilsson et al., 2019). If the best hit exhibited less than 97 % sequence similarity and less than 95 % coverage, only the best genus-level match was assigned. Species-level analyses combined operational taxonomic units (OTUs) into the genus of the best hit. Fungal genera were classified into ecological categories (e.g., white rot, brown rot, saprotroph, plant pathogen, ectomycorrhiza) based on Põlme et al. (2020). Fungal OTUs not assigned to a genus with known ecophysiology remained unclassified. The term "species" is used for both identified species from fruit body inventory and fungal OTUs, acknowledging that OTUs are putative species.

3.2.3.4 Data preparation

My analyses were based on community matrices derived from fruit body sampling and metabarcoding data for each year. I calculated the abundance of the fruit body community matrices as the sum of log segments occupied by each species. For the metabarcoding data, I determined abundance based on the number of reads, including only samples (logs in a given year) with a total read sum greater than 1,000 reads. I chose to analyze the data yearly because fungal communities are known to change throughout succession (Frankland, 1998; Fukami et al., 2010; Lepinay et al., 2021). As a result, the effects of fungal diversity on density loss may vary significantly between years. For instance, these effects could change systematically across successional stages, or particular communities at specific stages might be critical to explaining overall density loss. Analyzing aggregated data across years could obscure these biological effects, as contrasting effects among years might cancel each other out. To enhance the interpretability of the data, I conducted meta-analyses across the yearly models. Additionally, as an alternative approach, I aggregated species abundances and analyzed the overall communities.

In this study, I also used the Hill number approach (see Chapter 3.2.2.3) to estimate species diversity based on a standardized sample coverage for each log and year, utilizing the *estimateD* function within the R package ‘iNEXT’ (Hsieh et al., 2016). I used species richness (q=0), the exponential Shannon diversity index (q=1), and the inverse Simpson diversity index (q=2). To assess beta diversity, I calculated coverage-based dissimilarities along the Hill series for all community matrices using the *iNEXTbeta3D* function within the R package 'iNEXTbeta3D’ (Chao et al., 2023). The Hill numbers used for these calculations are based on the diversity indices described in Chapter 3.2.2.3.

3.2.3.5 Statistical analysis

I first analyzed all environmental variables to evaluate the relative importance of canopy cover, surrounding deadwood heterogeneity, surrounding deadwood amount, tree species, and fungal alpha and beta diversity on deadwood density loss. Tree species (beech vs. fir) and canopy cover (open vs. closed) were treated as factors, while deadwood amount and heterogeneity in the surroundings were standardized (z-transformed) continuous predictors. Since prior studies suggest that tree species strongly influence fungal alpha and beta diversity (Baber et al., 2016; Krah et al., 2018; Rieker et al., 2022), I analyzed beech and fir data separately to avoid confounding effects. Fir logs with fungal diversity measured via fruit body sampling in 2012 (n=5) were excluded due to insufficient sample size for reliable results.

I conducted structural equation models (SEMs) using the *sem* function within the R package 'lavaan' (Rosseel, 2012) to analyze alpha and beta diversity separately. SEMs assessed both the direct effects of environmental factors and fungal diversity on deadwood density loss, as well as indirect environmental effects mediated by fungal diversity. Deadwood density loss (a proportional variable with values between 0 and 1) was arcsin-transformed for normal distribution, and species alpha diversity (used as both a response and predictor) was $\log_{10}$-transformed. For beta diversity, I performed Principal Coordinates Analyses (PCoA) for each species dissimilarity matrix of each Hill number, using the *cmdscale* function within the R package 'stats.' I used the species scores of the first two PCoA axes, representing community composition, as predictors without further transformation. I applied SEMs to each annual combination of sampling method and diversity index (q0, q1, q2). These analyses covered both alpha diversity (estimated species diversity) and beta diversity (community composition). To account for the nested design, I incorporated the site as a predictor in all models.

I synthesized the results across years by performing meta-analyses on the outputs of the annual alpha and beta SEMs. Using the *metagen* function within the R package 'meta' (Schwarzer et al., 2015), I combined the estimates and standard errors from the annual models to calculate overall effect sizes for the direct and indirect effects on deadwood density loss for each sampling method and diversity index.

I assessed the robustness of the SEM models by applying additional single models. (i) For deadwood density loss, I conducted beta regression models (beta-distributed data: 0,1) using the *gam* function within the R package 'mgcv', specifying with the argument family = betar(link = 'logit'). The same predictors as in the SEMs were included, with the site as a random effect to account for the nested study design. Although some plots contained both

beech and fir logs (six plots), including plot nested within the site as a random effect led to singular fits due to the small sample size. Since model performance was similar, I reported results using the site as the random effect. (ii) I also conducted linear mixed-effects models using the *lmer* function within the R package 'lmerTest' (Kuznetsova et al., 2017). Here, fungal diversity was the response variable, environmental variables were predictors, and site was included as a random effect. To normalize the data, I $\log_{10}$-transformed estimated species diversity (alpha diversity) and used raw scores from the first two PCoA axes for beta diversity, as they were normally distributed. These models were applied separately for each annual combination of sampling method and diversity index (q0, q1, q2).

As a final step, I aggregated communities across years by summing species abundances. For metabarcoding data, I used incidence data, where OTU abundance was based on the number of years it appeared in the dataset since read counts do not reflect true species abundances. Before aggregation, I rarefied the yearly community matrices (minimum read sums: 887 for beech, 1129 for fir) to minimize biases from varying sequencing depths that could impact OTU detection and subsequent incidence and abundance estimates.

4 SYNOPSIS OF THE MAIN RESULTS AND DISCUSSION

4.1 Objective I: How do stand- and object-scale factors affect internal temperature dynamics in deadwood, and do their contributions differ between monthly and seasonal scales?

In general, the recorded highest mean daily internal deadwood temperature was 31.42 °C in August 2017, while the lowest was -10.12 °C in February 2018. During these months, the extreme temperatures included a minimum of -17.31 °C (February 2018) and a maximum of 49.65 °C (August 2017). The analyses of environmental factors (canopy cover, surrounding deadwood amount) and object-scale factors (tree species identity, diameter, position) influencing the internal deadwood mean, minimum, and maximum temperatures revealed that canopy cover had the strongest overall effect on deadwood temperatures, whether examined at monthly or seasonal levels.

At the monthly level, deadwood logs in open canopies were characterized by higher daily mean temperatures (June-August, on average +2 °C) and maximum temperatures (May-September, on average +6.39 °C), as well as lower daily minimum temperatures (February-November, on average -2.08 °C) compared to those in closed canopies (Figure 2). However, the models based on monthly aggregated data (used as a sensitivity analysis to account for temporal autocorrelation observed in the models based on daily resolution, see Section 3.2.1.3) did not support these effects for minimum temperatures in February, March, and May (Table 1). In October and December, daily mean and in December daily maximum temperatures were significantly lower in open compared to closed canopies.

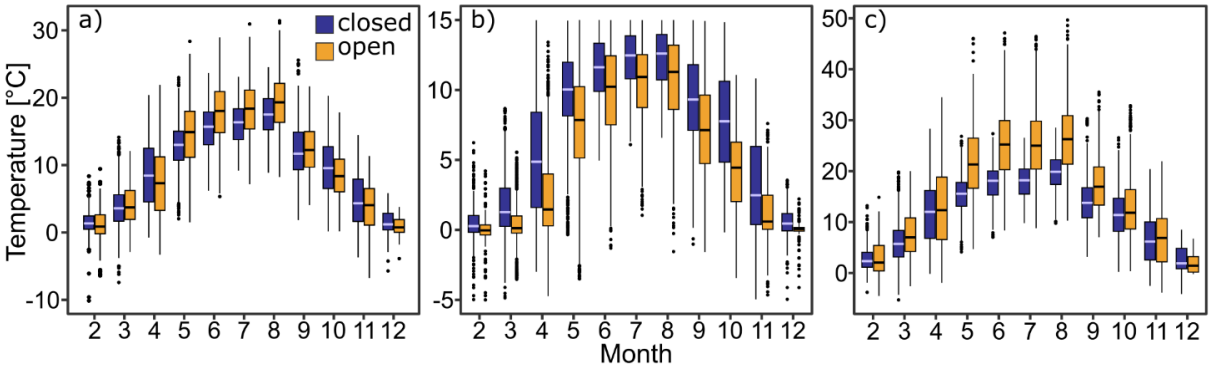

Figure 2: Boxplots of daily a) mean, b) minimum, and c) maximum temperatures inside deadwood logs under open and closed canopies in each month of 2017 and 2018 (most complete data). Note that in December, only values from 2018 are presented, due to missing data in 2017. January is not shown due to unreliable data caused by the high number of days with snow cover (see Section 3.2.1). Adapted from Schreiber et al. (2025a) (Manuscripts 10.1).

In addition to canopy cover, the surrounding deadwood amount influenced daily mean temperatures negatively in June and July. Tree species identity also affected deadwood temperature, with fir deadwood showing lower daily mean temperatures (June-August, on average -0.96 °C) and lower daily maximum temperatures in August compared to beech deadwood (Figure 2). However, the effects of deadwood amount and tree species identity were not supported by models based on monthly aggregated data (Table 1).

The seasonal models, which divided the years into a growing season (May-October) and a winter season (November-April), also highlighted canopy cover as the most important factor influencing deadwood temperature. Daily mean and maximum temperatures were significantly higher in open canopies (+1.12 °C) during the growing season, and for daily maximum temperatures, also during the winter season (+1.87 °C) (Figure 2). However, the effect on daily maximum temperature was stronger during the growing season (+5.05 °C). Daily minimum temperatures were significantly lower in open canopies compared to closed canopies in both seasons (winter: -1.80 °C, growing season: -2.81 °C) (Figure 2, Table 1). Additionally, in the growing season, fir deadwood had lower daily mean and maximum temperatures, and daily maximum temperatures were also significantly lower on plots with high surrounding deadwood amounts (Table 1).

Table 1: T-values (predictor estimate divided by SD) of the a) monthly and b) seasonal models testing stand- and object-scale factors on deadwood mean, minimum and maximum temperature. A positive t-value indicates higher temperature values in the reference group (open canopy, uplifted position, fir deadwood) or an increase in temperature with increasing deadwood amount or object diameter. Conversely, a negative t-value indicates lower temperature values in the reference group or a decrease in temperature with increasing deadwood amount and object diameter. Values in bold represent significant effects (: p<0.05, **: p<0.01, ***: p<0.001). The marginal R^2 represents the explained variance by the fixed effects (stand- and object-scale variables) in each model. Models are based on the years 2016-2019. Seasons were defined based on biological data of the study area (see Section 3.2.1.3). Note that January is not shown due to unreliable data caused by the high number of days with snow cover. Adapted from Schreiber et al. (2025a) (Manuscripts 10.1).*

a)		Canopy (reference "open")			Deadwood amount			Object diameter			Position (reference "uplifted")			Tree species (reference "fir")			Marginal R^2		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Month	2	-1.95	**-2.49***	-1.25	1.06	1.9	-0.21	-0.77	-0.74	-0.74	-0.39	-1.37	1.32	-0.79	-1.2	-0.09	*0.14*	*0.20*	*0.06*
	3	-1.34	**-3.88****	-0.12	-0.82	-0.54	-1.29	0.9	-0.25	0.75	0.86	-0.24	0.88	-0.56	-1.42	-0.44	*0.36*	*0.25*	*0.35*
	4	-0.03	**-8.36*****	1.35	-0.14	-1.3	-0.92	1.31	0.71	-0.3	1.39	0.88	0.5	-0.98	-0.91	-0.48	*0.02*	*0.22*	*0.03*
	5	1.01	**-2.87***	**4.12****	-0.77	-0.37	-0.27	0.55	0.98	-0.17	0.89	0.88	0.64	-1.24	-0.94	-1.44	*0.28*	*0.29*	*0.24*
	6	**6.98*****	**-3.94****	**4.39****	**-3.68****	-0.4	-0.21	0.1	1.41	-0.44	1.8	0.36	1.31	**-2.66****	-0.8	-1.42	*0.14*	*0.23*	*0.25*
	7	**4.12****	**-3.57***	**4.24****	**-2.68***	-0.28	-0.03	-0.18	0.89	-0.55	1.27	0.09	0.52	**-2.45***	-1.17	-1.81	*0.18*	*0.24*	*0.30*
	8	**2.66***	**-5.12****	**3.72****	-0.99	-0.39	0	0.02	1.36	-0.87	0.58	-0.09	0.79	**-2.17***	-1.65	**-2.03***	*0.13*	*0.25*	*0.27*
	9	0.52	**-9.93*****	**8.02*****	-0.09	-0.35	-2.22	0.81	1.4	-0.34	0.05	-0.6	0.56	-0.92	-0.52	-1.73	*0.05*	*0.16*	*0.18*
	10	**-2.51***	**-4.33****	0.4	0.15	-0.04	-1.25	**2.14***	0.36	-0.81	0.92	-0.47	0.64	-1.01	-1.06	-0.94	*0.16*	*0.23*	*0.12*
	11	-1.49	**-5.07****	0	-0.42	-0.18	-0.68	0.32	0.26	0.55	0.26	-0.59	0.95	-0.09	-0.35	-0.08	*0.37*	*0.31*	*0.36*
	12	**-3.24***	-2.33	**-2.67***	-0.04	1.16	-1.3	-0.62	-1	-0.1	-1.1	-1.59	-0.29	-0.09	-1.45	0.93	*0.08*	*0.12*	*0.05*
b)																			
Season	Winter Nov-Apr	0.3	**-7.73*****	**2.91***	-0.75	0.73	-0.91	-0.17	0.11	-0.33	-0.55	-1.35	-0.5	-1.18	-1.78	-0.65	*0.06*	*0.14*	*0.07*
	Growing season May-Oct	**6.57*****	**-9.87*****	**20.47*****	-1.92	-0.79	**-3.83****	-0.34	1.37	-1.74	0.71	-0.31	1.95	**-2.29***	-1.13	**-4.09*****	*0.11*	*0.12*	*0.17*

4.1.1 Canopy cover as the main driver of internal deadwood temperature

Across all months and seasons, canopy cover was the main driver of internal deadwood temperature, with a generally greater variation in microclimates in open canopies, with lower minimum temperatures and higher maximum temperatures during the growing season. These effects can be explained by the buffering capacity of temperatures of intact and closed forest canopies (De Frenne et al., 2019; Thom et al., 2020; Zellweger et al., 2020). The intact forest canopy shelter the ground from solar radiation (Graham, 1925; Lindman et al., 2022) and mitigates temperature extremes through increased evapotranspiration during hot and dry conditions (Thom et al., 2020). The results confirm that canopy cover buffers microclimate extremes, with stronger effects in the leaf-on phase (summer) than in the leaf-off phase (winter) in broadleaf stands (Zellweger et al., 2019). However, my results also showed that closed canopies reduce minimum temperatures in winter, indicating year-round buffering effects.

The strong link between deadwood temperature and canopy cover enables predictions about the potential impacts on biodiversity and decomposition processes in the context of climate change. One could anticipate that deadwood in our forests will face higher temperatures in the future. Thus, on the one hand, higher temperature can increase heterotrophic respiration and thus deadwood decomposition (Forrester et al., 2012; Herrmann and Bauhus, 2013; Mackensen et al., 2003; Russell et al., 2014; Seibold et al., 2021), which will be discussed in more detail in Chapter 4.3, and on the other hand higher and more extreme temperatures might exceeding the physiological tolerance of deadwood organisms (Maynard et al., 2019; Stokland et al., 2012). This might result in changing species diversity patterns and thus may alter related ecosystem processes via metabolic constraints. However, previous studies showed, that the community composition of wood-decomposer species (beetles and fungi) differs between open and closed canopies under current conditions (Krah et al., 2018; Seibold et al., 2016b), indicating that decomposer communities are associated with different microclimatic conditions (Boddy and Heilmann-Clausen, 2008; Fukasawa, 2021). With increasing temperatures, decomposition rates could increase in the future, thereby enhancing the carbon and nutrient cycles in temperate forests (Crockatt and Bebber, 2015; Eichenberg et al., 2017), however, moisture may become a limiting factor in the future due to alternated precipitation patterns, potentially reducing decomposition rates (Oberle et al., 2018; Seibold et al., 2021).

4.1.2 Minor effects of deadwood amount, diameter, position, and tree species on internal deadwood temperature

The surrounding deadwood amount showed only weak negative effects on deadwood temperature, contradicting my assumption, that higher deadwood amounts lead to higher internal deadwood temperature due to a lower albedo (Cherubini et al., 2012). I acknowledge that the sample size for the predictor variable, deadwood amount, was unbalanced in this study. However, given the low heteroscedasticity in the models, I conclude that the effect of deadwood amount on deadwood temperature is negligible at the scale of this research. This is in line with previous studies, which also found no significant effect of deadwood amount on the surrounding air temperature in forest stands (Haughian and Frego, 2017; Kovács et al., 2017; Thom et al., 2020).

Deadwood diameter only showed weak and non-significant tendencies for slightly higher minimum temperature in objects with larger diameters in the growing season, when raw data was plotted (see supplementary materials of Manuscripts 10.1). I expected that larger objects would exhibit greater thermal inertia, leading to variations in temperature based on the object's diameter. The weak and non-significant effects may result in the fact that only CWD objects were considered in this study. However, the diameter variation of the objects varies considerably between 19-47 cm, with more than 65 % of the objects having diameters above 30 cm. This limited range may not provide enough variability, especially considering that in the study by Pouska et al. (2016), which found that temperature stability increased with diameter, the diameter range was 10-103 cm. In my study, the temperature was measured 5 cm below the surface at the cross-section end. This standard depth likely amplified the influence of surrounding air temperature, potentially masking any effects of diameter variability. Walczyńska and Kapusta (2017) found that deeper measurements in stumps increased minimum temperatures and reduced variation in winter, emphasizing the importance of measurement depth for assessing deadwood’s temperature buffering.

Furthermore, the analyses revealed, that deadwood position had no significant effect on internal deadwood temperature. This contrasts with the study by Lindman et al. (2022), who found that standing deadwood was warmer than lying deadwood. The difference might be explained by differences in exposure to radiation, as Lindman et al. (2022) studied vertically standing deadwood, while uplifted objects in my study remained horizontal. Additionally, in the study by Lindman et al. (2022), lying logs could be covered by near-ground vegetation. In contrast, my plots were standardized to eliminate variation in vegetation cover through annual mowing,

ensuring that both lying and uplifted objects received similar sunlight exposure, which may explain the differing results.

Lastly, mean temperatures were significantly lower in fir than in beech deadwood during warmer months (June - August) and the growing season. Since physical properties or surface characteristics (e.g., bark cover or color) were not measured, I can only speculate on the causes. It might be that different deadwood temperatures result from differences between angiosperm and gymnosperm wood characteristics. Fir wood is generally less dense than beech (Petritan et al., 2023), which may explain the lower heat absorption and storage, as less dense wood has reduced thermal conductivity (Suleiman et al., 1999). Differences in bark (partly or completely debarked due to decomposition) and wood color (i.e., lightness), which affect heat absorption, may also play a role. Fungal colonization can further influence wood color; for instance, white rot fungi produce lighter colors as cellulose, which appears white, remains after lignin decay (Fukasawa, 2021). In contrast brown rot wood appears darker as lignin persistent after cellulose decay (Fukasawa, 2021). Both beech and fir can be affected by white and brown rot fungi, with the prevalence of fungal species exhibiting specific decay characteristics depending on various factors, such as environmental conditions and stochastic processes (Boddy, 2001; Brabcová et al., 2022). Furthermore, differences in physical wood characteristics caused by specific decay processes can be related to differences in the water-holding capacity of the deadwood object (Přívětivý and Šamonil, 2021). Thus, fir may retain more moisture than beech, which could buffer temperature extremes in the growing season (Davis et al., 2019). Additionally, observations suggest that bryophyte cover was higher on fir, which may enhance moisture retention and cooling (Heilmann-Clausen and Christensen, 2005; Pouska et al., 2017). However, further research is needed to investigate how deadwood properties, surface structure and color changes, and decay processes affect internal temperatures (see Chapter 5.4).

4.2 Objective II: How do contrasting microclimatic conditions affect wood-inhabiting fungi's successional trajectory and diversity patterns on deadwood?

Over ten years of fungal species succession during deadwood decomposition, colleagues identified 486 species across tree species (beech and fir) and deadwood sizes (FWD and CWD). Up to 25 % of the species were unique to either the open or closed canopy conditions, while more than 50 % were found in both microclimates (Figure 3). For more details, Manuscripts 10.2 provides additional results highlighting the top two species found exclusively under each canopy type or both, along with their incidence frequency over time. It also includes a table of species exclusive to each canopy treatment within two-year time windows, identifying the most relevant species for each canopy condition.

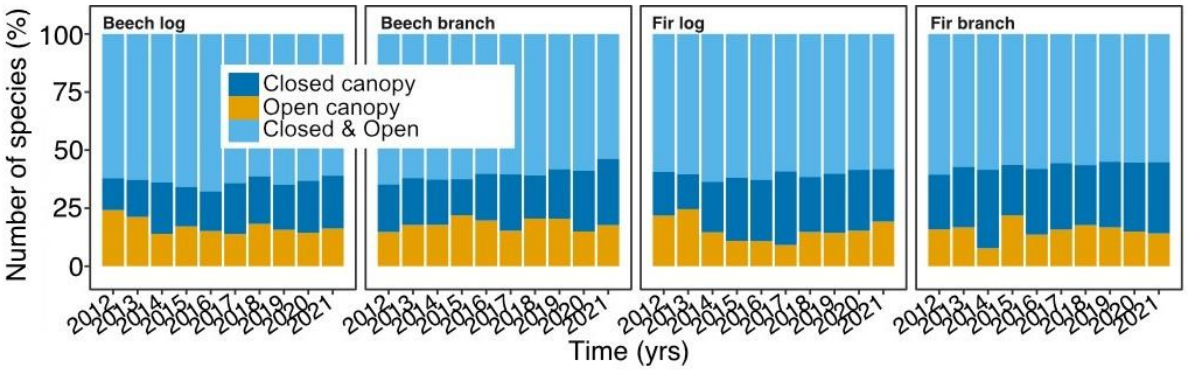

Figure 3: Scaled number of species found either uniquely or shared under the canopy treatment. Adapted from Schreiber et al. (2024) (Manuscripts 10.2).

Although I observed an increasing trend in treatment-based alpha diversity for logs and branches of both tree species over time, no significant interaction between time and microclimatic conditions was detected. Nevertheless, when response trends and confidence intervals were considered, the temporal response of fungal diversity differed between microclimatic conditions (Figure 4). In the first years of succession, treatment-based alpha diversity of common and dominant species showed similar trends but differed and showed diverging trends in later years between both canopies. In later years, common and dominant species showed lower alpha diversity in open compared to closed canopies. These trends were not shown for rare species, which showed almost non-distinguished trends between open and closed canopies. For beta diversity, I detected mostly non-significant trends over time, with dissimilarity values around 0.25 between microclimates on logs of both tree species and beech branches. Fir branches showed higher dissimilarity values, particularly for common and

dominant species. Overall the dissimilarity of rare species between the microclimates was lower compared to common and dominant species.

The lack of clear differences in the treatment-based alpha diversity between closed and open canopies aligns with a study by Vogel et al. (2020), which examined diversity patterns of saproxylic beetles, wood-inhabiting fungi, and spiders across different microclimates during the early decay stages (first four years) of six tree species. Similar to my findings, Vogel et al. (2020) reported no significant differences in alpha diversity between canopy treatments for beech and fir deadwood. However, in the later stages of succession, I observed emerging trends toward differences in alpha diversity between closed and open canopies, which will be discussed in the following sections.

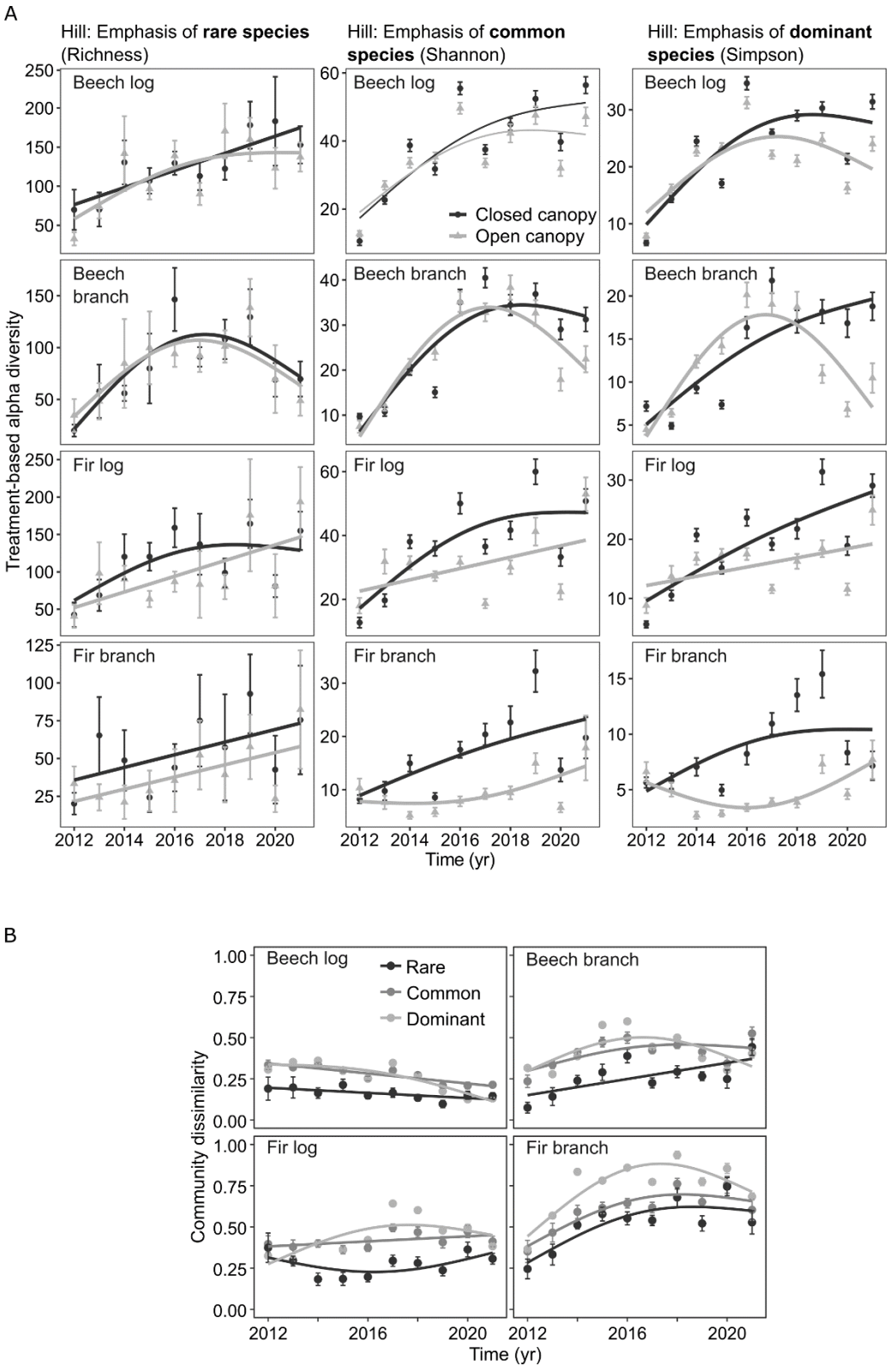

Figure 4: A: Treatment-based alpha diversity of fungal fruiting communities under closed (black) and open (grey) canopy treatments with time in years. B: Treatment-based community dissimilarity of fungal communities between canopies with time in years. In both A and B, smooth curves represent generalized additive model (GAM) fits, with error bars showing 95 % confidence intervals. Adapted from Schreiber et al. (2024) (Manuscripts 10.2).

4.2.1 Fungal fruiting under variable microclimatic conditions

Fruit body development is influenced by macroclimatic and meteorological factors (Büntgen et al., 2012; Kauserud et al., 2008; Krah et al., 2023; Salerni et al., 2002; Sato et al., 2012), primarily driven by high summer precipitation and cooling temperatures in fall (Boddy et al., 2014). Climate warming is shifting fruiting patterns toward longer fruiting seasons (Boddy et al., 2014). In an earlier phase (2012-2015) of the same experiment, colleagues and I observed that species fruiting in open canopies were more characterized by tougher fruit bodies compared to those in closed canopies, presumably as an adaptation to reduce water loss (Krah et al., 2022). However, fruit body size showed inconsistent results between lineages, with larger fruit bodies of Basidiomycota communities and smaller fruit bodies of Ascomycota communities in open canopies. Smaller fruit bodies are hypothesized to dissipate excess heat more rapidly, according to the heat-up-cool-down hypothesis, potentially reducing heat stress under open canopies (Krah et al., 2022). The third trait that we analyzed, fruit body color lightness, showed significant results only for Basidiomycota communities, which produced lighter fruit bodies in open canopies on beech deadwood (Krah et al., 2022).

Notably, I found only one species, *Hypholoma marginatum*, that produced soft-fleshed fruit bodies in open canopies during years 3-4. In later years, no soft-fleshed fruiting species were present in open canopies, while several species (*Entoloma cetratum*, *Mycena zephirus*, *Psathyrella obtusata*, *Pholiota limonella*, *Simocybe coniophora*) continued to fruit with soft-fleshed bodies under closed canopies. This suggests that environmental conditions in open canopies limit the development of fruit bodies with higher water demands. However, further analyses are needed to understand the morphological adaptations of fungal fruit bodies under different microclimatic conditions (see Chapter 5.4).

Additionally, it remains unclear whether species were present as mycelium but unable to fruit due to unsuitable environmental conditions, or if they were entirely lost from the substrate. This could be investigated by estimating the presence of fungal mycelium using metabarcoding of RNA or metatranscriptome analysis. Species with higher read counts from environmental sequencing approaches tend to produce many fruit bodies (Ovaskainen et al., 2013). However, this study also revealed that some highly abundant species detected through sequencing were rarely observed in the fruit body record. Conversely, another study found that certain rare fungal species were only detected through fruit body sampling and not through environmental samples or metabarcoding (Frøslev et al., 2019). To capture the fullest diversity of species, an ideal approach would combine both environmental sequencing and fruit body sampling (Rieker et

al., 2024). Fruit bodies form only when the physiological and nutrient conditions of the mycelium, along with environmental factors, are suitable (Kües and Liu, 2000). The fruiting community likely represents a subset of species present as vegetative mycelium. The observed decline in fruiting or species loss in later years may suggest shifts in successional trajectories.

If harsh environmental conditions reduce species diversity, it remains unclear why this primarily occurs in later decay stages. One possible explanation is the dominance-tolerance trade-off (Maynard et al., 2019) among secondary colonizers. This concept suggests that wood-inhabiting fungi either have narrow environmental tolerance with strong competitive abilities, or broader tolerance but weaker competitive capacity. Primary and early secondary colonizers, which succeed endophytic fungi that inhabit living trees, require strong competitive abilities (Hiscox et al., 2015) but may have reduced tolerance to microclimatic fluctuations. As decay progresses, later-stage colonizers may need even greater competitive abilities to outcompete established species, but their lower environmental tolerance may hinder growth under open canopy conditions, which may explain the decline in alpha diversity.

4.2.2 Microclimatic fluctuations as a driver of fungal diversity

In my study, I observed lower diversity in later decay stages under open canopies (with more fluctuating conditions), but not in early decay stages. A previous study using microcosms showed that increasing temperature fluctuations enhanced species richness due to niche differentiation (Toljander et al., 2006). My findings partly contrast with this, suggesting that microclimatic fluctuations affect species diversity differently across succession stages. Whether environmental fluctuation leads to an increase or decrease in diversity is one long-lasting question in ecology (Bernhardt et al., 2020; Rashit and Bazin, 1987). For example, Rapoport's rule suggests that species tend to have higher species ranges in northern areas (Stevens, 1989). One explanation for this pattern is that species are more adapted to intense seasonality, making them more tolerant towards changing conditions or fluctuation on smaller temporal scales. This is supported by a study of global soil fungi, which showed that species ranges are larger towards higher altitudes (Tedersoo et al., 2014). For fungi, higher phylogenetic diversity has been linked to greater thermal seasonality across Europe (Bässler et al., 2022). Environmental fluctuations can lead to variable diversity responses across organism groups, with plankton diversity decreasing (Gonzalez and Descamps-Julien, 2004), while bacteria and wood-inhabiting fungi show increased diversity (Nguyen et al., 2021; Toljander et al., 2006). To further investigate the potential effect of microclimatic fluctuations on fungal species diversity across succession, an experiment could examine how established fungal communities respond to sudden shifts

from stable to fluctuating conditions, such as transferring communities from closed to open canopies across different decay stages. Furthermore, my findings are restricted to temperate regions and may not apply to climates with more stable conditions, such as humid tropics. Additional experiments in diverse biomes would enhance our understanding.

However, my results showed that alpha diversity had stronger patterns when common and dominant species were considered, compared to rare species. This suggests that rare species may be more tolerant of microclimatic fluctuations across successional stages, indicating that Rapoport's rule might primarily apply to dominant species. Additionally, by analyzing both FWD and CWD from beech and fir, I found greater divergence in alpha diversity between canopy conditions over time, particularly in branches compared to logs. On the one hand, this might be the results, because logs and branches harbor significantly different fungal fruiting communities when their surface area is standardized (Krah et al., 2018). Thus, fungal fruiting communities on branches, which decompose faster and reach advanced decay stages earlier, are more sensitive to open canopy conditions. On the other hand, as alpha diversity differences in logs also increased over time, these effects may become more pronounced in later decay stages. Thus, fungal data of long time series under standardized conditions are necessary to further illuminate these diversity patterns.

4.2.3 Deadwood decomposition in different microclimates

Another possible explanation for the reduced alpha diversity under open canopies is the difference in decay rates (successional speed) and moisture content between deadwood in open and closed canopies. Decomposition occurs faster under open canopies (Griffiths et al., 2021; Jacobs and Work, 2012; Janisch et al., 2005; Shorohova and Kapitsa, 2014); however, the relationship between fungi and decomposition remains unknown and will be discussed in Chapter 4.3. Additionally, the moisture content in deadwood generally increases during succession (Pichler et al., 2012; Přívětivý and Šamonil, 2021), though this has not been thoroughly studied across different microclimates. Therefore, the observed differences in diversity between canopy conditions may reflect variations in decay rates or moisture dynamics. This suggests that if the decay stage, rather than time, is used as a predictor, no significant diversity differences between canopies might be found. My results showed non-significant interactions between decay stage and canopy treatment on alpha diversity, and no significant trends in beta diversity (see supplement of Manuscripts 10.2). However, decay rates were not directly measured (e.g., via mass loss), but instead assessed using a four-class visual classification system for deadwood, which is effective for detecting coarse differences in

decomposition (Köster et al., 2015; Sandström et al., 2007) without disrupting the successional process. The deadwood objects exhibited considerable variation, with some advancing to decay stages three and four.

Additionally, my study is limited by not capturing the full successional trajectory of fruiting fungal diversity. Nonetheless, it spans 10 years of species succession on the same deadwood objects, providing an exceptional timeframe for studying fungal species succession.

4.3 Objective III: How do stand-scale environmental factors and wood-inhabiting fungal diversity directly and environmental factors indirectly affect deadwood density loss via fungal diversity?

After ten years of decomposition, log density loss ranged from 0.04 % to 80 %. Annual models and meta-analyses from both sampling methods (fruit body survey and metabarcoding) consistently identified tree species as the main driver, with significantly higher density loss in beech logs than fir logs. Canopy cover also had a strong effect, with greater density loss under open canopies compared to closed canopies (Figure 5).

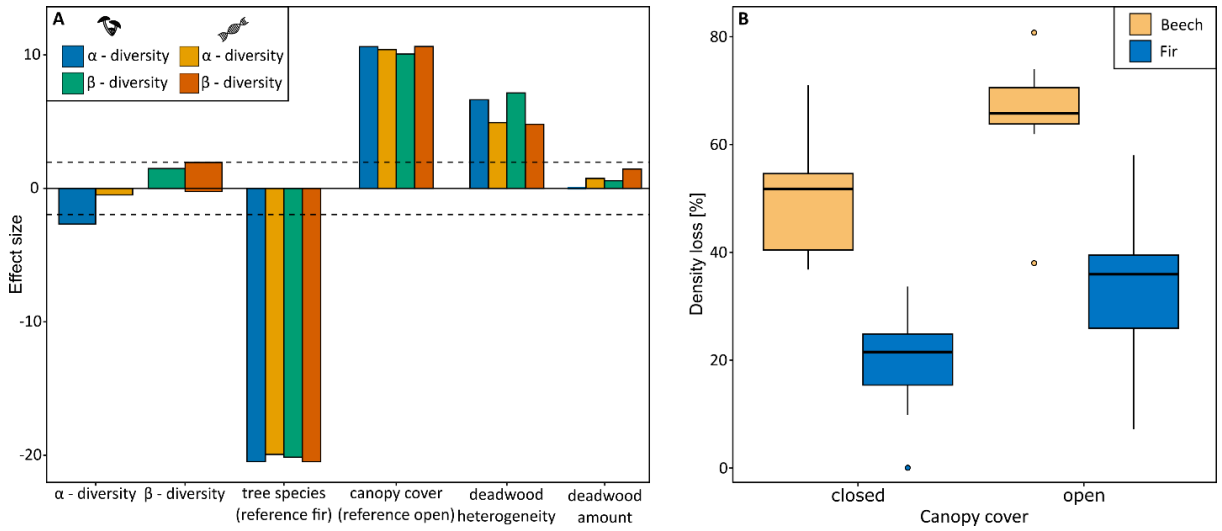

Figure 5: A: Effect size (z-value) of environmental factors on deadwood density loss for alpha and beta diversity (q0 values) across each sampling method, determined through meta-analyses based on annual structural equation models. Dashed lines indicate the significance thresholds (z-values >|1.96|). B: Raw plots showing density loss for each tree species (yellow: beech, blue: fir) under different canopy covers after ten years of decomposition. Adapted from Schreiber et al. (2025b) (Manuscripts 10.4).

The results in the following section refer unless explicitly stated otherwise, to the findings of the meta-analyses of the annual SEM models. The results of the annual SEM models, the models using aggregated data, and the raw data plots referenced in the following paragraphs are provided in the supplementary materials in Manuscripts 10.4.

4.3.1 Impact of environmental factors and fungal diversity on deadwood density loss

Canopy cover was consistently identified as the most important driver of deadwood density loss across all models, with a higher loss under open canopies compared to closed canopies (Figure 5). This finding was largely consistent across the annual models and the aggregated data models at the alpha diversity level, as well as in the majority of models at the beta diversity level. An exception was noted for fruit body sampling on beech, where canopy cover emerged as the second most important driver. The plots of the raw data supported these patterns irrespective of tree species or sampling method.

Deadwood heterogeneity in the surrounding significantly influenced the density loss of beech logs across all diversity measures (q0, q1, q2) at both alpha and beta diversity levels, for both metabarcoding and fruit body data (Figure 6). This effect was evident in raw data and supported by both annual models and aggregated data models, except for beech metabarcoding data annual models 2015 (beta regression models) and 2021 (SEM). Beech logs on plots with higher deadwood heterogeneity showed higher density loss. Deadwood heterogeneity did not have a significant effect on the density loss of fir logs.

The surrounding deadwood amount had no significant effect on density loss of beech logs and showed only small, and inconsistent significant effects on density loss of fir logs. Annual models indicated that these effects were driven by a single year, while meta-analyses revealed no consistent patterns for fir. Effects were either absent in the annual models (fir metabarcoding) or limited to a single year (2013, fir fruit body sampling).

Fungal alpha diversity had significant direct effects on deadwood density loss. On beech logs, higher richness of rare, common, and dominant species based on metabarcoding data increased density loss, while higher fruiting species richness of dominant species (q2) reduced density loss. For fir logs, higher fruiting species richness of rare and common species (q0, q1) reduced density loss (Figure 6). At least one annual model supported these findings, but aggregated data models only confirmed effects for fir. Community dissimilarity effects based on the meta-analysis were not supported by the annual models, except for common species detected via fruit bodies on beech logs.

4.3.2 Effects of environmental factors on fungal diversity

The meta-analyses identified canopy cover as the main driver of fungal diversity across tree species and sampling methods (Figure 6). I observed higher fungal species diversity (rare, common, and dominant species) under open canopies on fir logs (metabarcoding) and beech

logs (fruit body sampling) (Figure 6), though this effect was weak when focusing on the raw plots. Furthermore, dissimilarity of rare (q0) and common (q1) species communities was affected by canopy cover, whereas dominant species dissimilarity (q2) was not affected, except for communities detected on fir logs via fruit body sampling. These effects were supported by most annual models and raw plots.

Deadwood heterogeneity showed minor effects on fungal diversity, except for the alpha diversity of rare species detected via fruit body sampling on fir logs, where a positive effect was observed (Figure 6). Furthermore, deadwood heterogeneity showed a significant effect on the dissimilarity of dominant species on beech logs (metabarcoding) and fir logs (fruit body sampling) (Figure 6). However, these effects were limited to specific years in the annual models (LMER and SEM).

Surrounding deadwood amount weakly increased alpha diversity for rare, common, and dominant species in fruit body data on beech logs. By contrast, the opposite pattern was observed for species detected via fruit body sampling on fir logs, where surrounding deadwood amount had weak negative effects on the alpha diversity of rare, common, and dominant species. These patterns were inconsistent across annual models and not supported by models with across years aggregated data or raw plots. Similar inconsistencies were noted for common species dissimilarity on beech logs (fruit body sampling) and dominant species dissimilarity for fir logs (fruit body sampling).

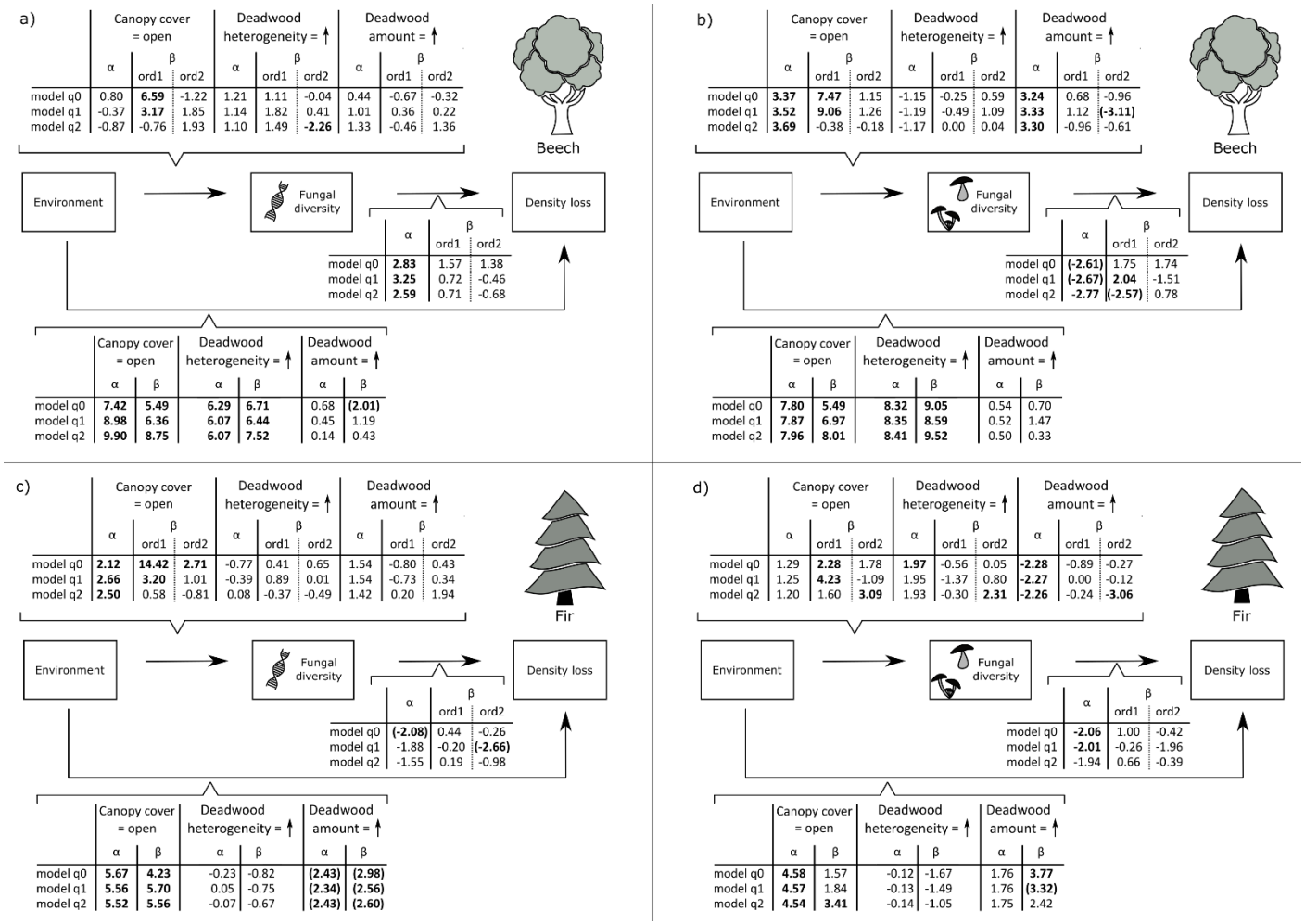

Figure 6: Effect sizes (z-values) of the meta-analyses of structural equation models (SEM) for alpha and beta diversity (Hill numbers: q0, q1, q2). For each tree species (beech, first row a) and b); fir second row c) and d)) and sampling method (metabarcoding, first column a) and c); fruit body, second column b) and d)), annual SEMs were meta-analyzed, resulting in effect sizes for each diversity measure (model q0, model q1, model q2). Arrows indicate the tested effects of canopy cover, deadwood heterogeneity, and deadwood amount on fungal diversity, as well as their direct and fungal diversity–mediated effects on density loss. Upward arrows for deadwood heterogeneity and amount indicate that positive z-values correspond to increases in fungal diversity or density loss with increasing predictor values. Beta diversity is represented by the first two principal coordinates analysis (PCoA) axes (first axis: ord1; second axis: ord2). Significant effects (|z|>1.96) are in bold; values in parentheses are not significant in at least one year based on the yearly-based SEM analyses and thus not interpreted.

4.3.3 Tree species and canopy cover mainly affect deadwood density loss

The results of my analyses showed that tree species was the main factor explaining deadwood density loss, which is in line with the results of studies identifying tree species as a major driver of deadwood decomposition (Harmon et al., 2020; Kahl et al., 2017; Kipping et al., 2022; Shorohova and Kapitsa, 2014; Weedon et al., 2009). My results align with these previous studies, demonstrating higher decomposition rates in angiosperm wood compared to gymnosperm wood, which can be mainly explained by differences in wood traits. Gymnosperms contain higher lignin concentrations and lower nitrogen and phosphorus levels, which slow their decomposition (Weedon et al., 2009). Additionally, the structural composition of lignin in angiosperms, with its higher proportion of sinapyl moieties, forms less densely cross-linked networks than the guaiacyl moieties predominant in gymnosperm lignin, making it more susceptible to chemical and enzymatic degradation (Brunow, 2001; Hatakka and Annele; Higuchi, 2006). Differences in hemicellulose composition and structural compounds within the tracheids of angiosperm and gymnosperm wood further influence decomposition (Weedon et al., 2009). My findings confirm that tree species traits outweigh environmental conditions, such as microclimate, and fungal diversity in explaining deadwood density loss.

Next to tree species identity, canopy cover emerged as a key predictor of deadwood density loss, ranking second in the overall models and first in tree species-specific models. Consistent with previous research, I found higher density losses under open canopies (Harmon et al., 2020; Janisch et al., 2005; Shorohova and Kapitsa, 2014). However, in my study, I was able to rule out potential masked effects by fungal diversity. Open canopies likely accelerate photodegradation and surface degradation by exposing deadwood logs to more solar radiation (Derbyshire and Miller, 1981; George et al., 2005) and increasing temperature variability, which promotes physical processes, such as frost cracking (Fravolini et al., 2018; Harmon et al., 1986; Russell et al., 2015; Zhou et al., 2007). Enhanced solar radiation may also degrade specific wood components, such as lignin, improving enzymatic accessibility for microorganisms and potentially accelerating decomposition (Austin et al., 2016). The plausibility of direct mechanisms associated with open canopies is further supported by the relatively weak indirect effects mediated through fungal diversity. Although canopy cover consistently influenced fungal community composition, the subsequent impact of these communities on wood density loss was minimal (see also discussion below). Discrepancies with the study by Janisch et al. (2005), which found minimal canopy effects, might result from their focus on early decomposition stages or shading by regrowth vegetation. In contrast, I ensured openness by annually mowing to prevent vegetation shading. Additionally,

macroclimatic conditions could influence canopy effects (Harmon et al., 2020), and for example, moisture availability may enhance or inhibit deadwood decomposition depending on whether it becomes a limiting factor (Seidbold et al., 2021). However, the study area is characterized by a high level of precipitation, and thus, moisture was likely not a limiting factor (see section 3.1.1).

My results showed that surrounding deadwood heterogeneity directly influenced deadwood density loss, with higher heterogeneity linked to higher deadwood density losses in beech. This effect cannot be attributed to fungal diversity, as I tested heterogeneity both directly and indirectly (via diversity) within one model. Thus, the assumption that habitat heterogeneity promotes diversity, which in turn affects density loss, was not supported. I can only speculate about the mechanism why deadwood heterogeneity in the surroundings increases deadwood density loss in beech. One possible explanation is that high heterogeneity plots often included additional fir logs, which might influence microclimate conditions beyond canopy cover. Fir decomposes more slowly than beech in my study, and observations suggest that fir retains more bark, which appears darker and may absorb more heat than the often-debarked and white rot-dominated beech logs. Thus, the presence of fir could raise microclimate temperatures and accelerate beech density loss for example through higher metabolic rates. However, this remains speculative. Additional data on microclimate and metabolic processes would be necessary to clarify these effects.

4.3.4 Limited effect of fungal diversity on deadwood density loss

My study found some significant effects of fungal diversity on deadwood density loss, but these effects were weak and inconsistent across tree species, diversity measures, and model approaches. Environmental factors consistently had stronger and more reliable effects. While many studies in the past have explored the relationship between fungal diversity and decomposition using chrono-sequence approaches (Rajala et al., 2011; van der Wal et al., 2015; Yang et al., 2024), there is still no consensus about the relationship between wood-inhabiting fungal diversity and decomposition processes (Runnel et al., 2024). Recent work has called for real-world studies that integrate natural fungal communities and a variety of diversity measures while accounting for both direct and indirect effects of the environment. With my study, I addressed this knowledge gap in biodiversity-ecosystem functioning (BEF) research, showing that environmental variability, such as canopy cover, is more important than fungal diversity in explaining deadwood density loss. This finding holds true across different diversity measures, whether focusing on alpha or beta diversity or considering rare, common, or dominant species.

My results suggest that from a highly diverse fungal species pool, distinct yet functionally redundant communities assemble under specific environmental conditions, consistently providing the capabilities (e.g., wood-degrading enzymes) needed for wood decomposition. However, this was clearly revealed by my structural equation models, which showed that fungal communities on beech and fir based on both, fruit bodies and metabarcoding, were strongly influenced by canopy cover. But, in turn, the composition of these communities was weakly associated to density loss.

However, my study has limitations. First, I measured deadwood density only after ten years, which limits insights into year-to-year decomposition dynamics. However, the data showed up to 80 % density loss over this period, indicating a broad range of variability, which allowed me to analyze decomposition effectively without the issue of fully decayed logs. Second, I calculated density loss using baseline values from the literature since no initial log samples were taken at the start of the experiment. While this approach may introduce some inaccuracies, such as underestimating density loss if initial wood density was atypical, it is unlikely to significantly affect my results, given the considerable variability observed across logs. For example, one exceptionally low-density loss value (<0.1 %) for a fir log could reflect an unusually high initial density due to competitive growth conditions. Third, I used subsamples from the edges of logs to assess density loss, which may not fully capture the spatial heterogeneity of decomposition within coarse woody debris (Pyle and Brown, 1999). I mitigated this by cutting slices from the edges before extracting the final disc and through the number of replicates in my study. Finally, I used deadwood density loss as a proxy for decomposition, acknowledging that it may underestimate certain aspects of decay, such as wood loss from the outer sapwood. Alternative measures, like changes in lignin and cellulose concentrations, could provide additional insights (Fravolini et al., 2018; Lombardi et al., 2013). However, density loss remains a practical and widely used parameter in comparable studies (Rajala et al., 2011; van der Wal et al., 2015; Yang et al., 2024).

5 SYNTHESES AND FUTURE PERSPECTIVES

Forest ecosystems face challenges by current and future climate change due to changes in air temperature and precipitation regimes as well as indirect factors such as increased disturbance events. These disturbance events are expected to alter microclimatic conditions within forest stands due to changes in canopy cover. Current studies have shown that changes in microclimatic conditions mainly affect deadwood processes such as decomposition as well as related wood-inhabiting fungal diversity (e.g., Shorohova and Kapitsa (2014), Krah et al. (2018)). Furthermore, additional stand-scale factors which may change with increased disturbance events such as deadwood amount and heterogeneity may change saproxylic species diversity (Lassauce et al., 2011; Seibold et al., 2016a; Seibold et al., 2016b) and thus deadwood decomposition. However, deadwood decomposition and related biological processes are manifold and complex. Thus, this dissertation contributes to disentangling the effects of environmental and object-scale factors on ecological processes in deadwood under varying microclimate.

5.1 Microclimate as the primary driver of deadwood processes

Among all studied environmental variables, the canopy-mediated stand-scale microclimate emerged as the most important factor influencing internal deadwood temperature and deadwood density loss. Furthermore, microclimate affects the succession and diversity of wood-inhabiting fungal species. This overarching pattern highlights the role of microclimatic conditions across multiple facets of deadwood processes and gives a comprehensive answer to my research questions (Chapter 2). My first study (Chapter 4.1) reveals that canopy cover is the most important factor influencing internal deadwood temperature, exceeding other environmental variables that may occur or fluctuate following disturbance events. These findings are attributed to the buffering capacity of intact canopies. Zellweger et al. (2019) demonstrated seasonal trends in microclimatic conditions under deciduous trees compared to areas outside forests, highlighting varying contributions of canopy cover, landscape, and topography in explaining minimum and maximum temperatures Although my three-year study did not account for landscape and topography, it included other stand-scale predictors and supports the observed seasonal trends. Notably, it identifies canopy cover as the main driver of internal deadwood temperature throughout the entire year (Chapter 4.1).

My second study (Chapter 4.2) on the succession of wood-inhabiting fungal species supports recent findings that microclimate affects wood-inhabiting fungal community composition.

However, most recent studies mainly focus on the initial years of deadwood decomposition and species colonization (e.g., Krah et al. (2018)). Due to the long-term deadwood experiment (10-year period), I can show, that after an increase in the first years a decreasing trend in fungal species diversity was observed in both open and closed canopies, but with a stronger decrease in open canopies (Chapter 4.2). However, the slopes of the diversity versus time relationship did not differ significantly between microclimate treatments. Still, the non-overlapping confidence intervals in many cases support the overall findings of lower species richness under open canopies. Nevertheless, the results lead to the conclusion that the fruiting of the fungal community on deadwood is mostly resilient against the predicted increase in canopy loss and thus microclimate changes.

Microclimate was also the major driver of deadwood decomposition processes, both directly and indirectly through changes in wood-inhabiting fungal communities (Chapter 4.3). While most research has primarily focused on only one of these processes, the interaction between decomposer communities and wood decomposition remains highly complex. Jacobs and Work (2012) provided initial insights, showing that density loss is influenced by both microclimate and decomposer communities. In my study (Chapter 4.3), I took this further by using structural equation models to simultaneously test these key relationships, revealing microclimate has the strongest direct and indirect effect, via wood-inhabiting fungal diversity, on density loss.

Overall, my studies show that the microclimate, which can be influenced by disturbances or forest management, is the most important factor among the tested variables influencing deadwood processes and the associated biological activities. This highlights the need to understand how climate change will influence deadwood processes, and how forest management strategies can be adjusted accordingly.

5.2 Impacts of climate change on deadwood processes

Disturbances are predicted to increase in temperate forests under future climate change. Windthrows and further disturbances result in a higher amount of deadwood in forest stands, which increases habitats for saproxylic fungi and beetles (Cours et al., 2022). Furthermore, windthrows lead to changes in canopy structure and thus changes in microclimate conditions affecting deadwood processes. More open canopies lead to an increase in mean temperature and more extreme temperatures (higher temperature in summer and lower temperature in winter) (Chapter 4.1), resulting in mainly increasing biological processes such as decomposition (Chapter 4.3). Thus, increased canopy disturbance and transformation of forest

ecosystems towards angiosperm trees, both forced by global warming, might cause higher rates of deadwood turnover. Increased decomposition in open canopies can accelerate the release of carbon stored in deadwood, potentially reducing carbon sequestration and increasing atmospheric carbon release. Which, in turn, could have positive feedback effects on climate change and accelerate these processes. However, processes in deadwood are difficult to disentangle as drivers are highly correlated. The predicted increase in temperature is connected with changes in precipitation regimes leading to an increase in drought events (Coppola et al., 2021). Thus, an increase in deadwood decomposition with increasing temperature is predicted as long as moisture is not limited (Baldrian et al., 2013). Deadwood moisture content is a critical variable as it is influenced by various factors such as precipitation, tree species identity, shading, ground contact, bark cover, lichen, and bryophyte cover (e.g. Harmon et al., 1986; Griffith and Boddy, 1991; Harmon and Sexton, 1995; Renvall, 1995). Although my findings showed that fungal fruiting is largely resilient to microclimatic changes (Chapter 4.2), fungal growth in deadwood depends on moisture content and inhibits whether the moisture level is too high or too low. Consequently, the survival of mycelia and the production of sexual reproduction organs (fruit bodies) of fungal species under future precipitation changes and prolonged drought events remain poorly understood (Lennon et al., 2012) and should be further investigated (more details in Chapter 5.4).

In the long term, changes in macroclimatic conditions are expected to drive a shift in tree species distribution across Central Europe, with species migrating poleward or to higher elevations (Hickler et al., 2012; Root et al., 2003). Since wood-inhabiting fungi are highly specific to their host tree species, such shifts in tree species may also alter the distribution of the associated fungi, potentially impacting ecosystem functions such as carbon and nutrient fluxes during decomposition processes across Europe. However, as these macroclimatic-driven changes in tree species distribution are expected over extended timescales, more immediate shifts in microclimatic conditions are likely to play a more significant role in influencing deadwood decomposition and saproxylic diversity patterns in the near future.

5.3 Implications for future deadwood management

Given the increasing pressures of climate change on forest ecosystems, there is broad consensus that adapting forest stands is essential to safeguard their resilience and ecological functions. Transforming current mostly monoculture stands into mixed stands with climate-adapted tree species increases resilience against the impacts of climate change (Bauhus et al., 2017). Additionally, structural diversity enhances forest resilience by creating varied microclimatic

conditions and microtopography, which can be facilitated through deadwood retention (Wijas et al., 2024). Currently, forest microclimates are primarily influenced by disturbance events and large-scale logging and thus open conditions, which significantly alter local conditions on stand and object scale (Blumröder et al., 2021, Chapter 4.1). My study has shown that key deadwood decomposers, wood-inhabiting fungi, are predominantly resilient to microclimatic changes, but also that a quarter of the species occur only under open or closed canopy conditions (Chapter 4.2). Therefore, it is important to enrich deadwood across different microclimates during management to support ecosystem functioning and enhance carbon and nutrient storage within forest stands.

Thus, future forest management strategies in Europe should focus on extending rotation lengths to enhance atmospheric carbon sequestration and support stable microclimatic conditions, as well as on increasing the quantity and quality of deadwood to improve habitats for biodiversity conservation (Oettel and Lapin, 2021, Chapter 4.2). Mixed forest stands, in particular, can enhance saproxylic diversity by supporting a broader range of host species. It is crucial to maintain and increase the diversity of deadwood within forests, considering factors such as varying dimensions, stages of decay, and microclimatic conditions, to support saproxylic communities and decomposition trajectory (Lassauce et al., 2011; Müller et al., 2020, Chapter 4.1-4.3). Consequently, the current pressure on forest ecosystems caused by disturbance events and an increase in deadwood could present an opportunity to foster the transition of forest ecosystems toward greater resilience.

5.4 Knowledge gaps and future research directions

In this dissertation, detailed analyses of within-deadwood temperature dynamics, the succession of fungal diversity, and environmental influences on decomposition highlight microclimate as the key factor affecting deadwood processes. With climate change expected to alter forest microclimates, shifts in deadwood microclimates, saproxylic diversity, and decomposition dynamics are inevitable. Nonetheless, further research, particularly long-term, real-world monitoring, is essential to better understand how these changes will impact the complex processes of deadwood decomposition. Given the strong interdependence between temperature and moisture content, future studies should prioritize disentangling their interactions, especially in the context of macro- and microclimatic influences. Microclimate should be considered in future research at both the stand and object scale.

At the stand scale, canopy cover is widely recognized as a major factor influencing internal deadwood temperature and subsequent decomposition processes (Chapters 4.1 and 4.3). However, other stand-scale variables that may shift with ongoing climate change, such as the quantity of deadwood due to increasing disturbance events (Patacca et al., 2023), remain underexplored. I studied these factors concerning internal deadwood temperature and deadwood decomposition, but further research is needed to disentangle factors such as the potential thermal absorption of varying deadwood amounts and their interactions with other drivers of forest microclimatic conditions beyond canopy cover, including understory vegetation, and soil structure.

At the object scale, further research should explore how deadwood properties, surface structure, color changes, and decay processes influence internal temperatures and metabolic rates. Since temperature is closely linked to moisture content (Pouska et al., 2016), a critical factor in deadwood decomposition and fungal growth, there is a need for more data from simultaneous measurements of internal deadwood temperature and moisture content to better understand their interaction. Measuring moisture in a heterogeneous log, however, presents challenges, as most studies rely on destructive methods, such as analyzing log disks in the laboratory. To address this, accurate and practical methods for real-world experiments are needed to measure both moisture and temperature in entire deadwood logs under various conditions. Future measurements should involve placing sensors at different depths and positions within logs, accounting for a wide range of diameters and environmental contexts. In addition to more precise measurements of temperature and moisture content, annual or decay-stage-specific measurements of deadwood density would enhance our understanding of how environmental effects and related diversity influence density loss throughout decomposition. This would further improve the findings of my third study (Chapter 3.2.3.2 and 4.3.4).

Although wood-inhabiting fungal communities are known to respond to microclimatic conditions, my study on the succession of fungal fruiting species revealed that community dissimilarity between harsh (open canopies) and benign (closed canopies) microclimates remains mainly stable over ten years (Chapter 4.2). However, at the alpha diversity level, we observed a decline in fungal species richness under harsh microclimates. This decline may persist or even intensify during later decay stages, underscoring the need for long-term fungal data sampled under standardized conditions to further illuminate these findings. Furthermore, future studies should aim to uncover why, and under what conditions, some fungi produce fruiting bodies while others do not. Experiments manipulating fungal communities under both stable and variable edaphic conditions could help test how interspecific competition between

tolerant, early-colonizing species and more competitive, later-stage colonizers influence fungal growth in harsh microclimates. Additionally, despite successful fruiting in specific environments, there is still limited understanding of the morphological adaptations and environmental cues that regulate fungal fruiting in response to variable microclimates.

My findings on fungal succession over ten years, based on fruit body data, also highlight the need for complementary sampling methods, such as metabarcoding, to confirm these results. Additionally, further research is essential to deepen our understanding of fungal mycelial resilience to extreme temperature and moisture conditions, as well as the adaptive mechanisms of fungal species at the fruit body level, given that fruit body production represents successful fungal reproduction. Also, to gain mechanistic insights into how fungal communities decompose wood, future studies should apply diverse methods to characterize active communities (e.g., via RNA analysis) and assess the actual abundance and functional performance of fungal individuals (e.g., using proteomics) in deadwood under specific environmental conditions. Moreover, the effects of microclimatic changes, particularly droughts, on bacteria remain unclear. Since bacteria are more climate-sensitive than fungi (Lennon et al., 2012) and play a significant role in deadwood decomposition (Stokland et al., 2012), additional research on their responses to shifting microclimates is crucial.

Summarizing these future research directions in the context of climate change highlights the crucial need to gain a deeper understanding of fungal responses to shifts in climate conditions. This involves investigating how projected changes in temperature and precipitation affect deadwood decomposition processes and the occurrence of fungal communities, both as mycelia and fruiting bodies, under controlled and standardized conditions. An experimental setup could be established where precipitation is varied not only in amount but also in frequency, simulating potential drought conditions. This could be achieved by using roofs to cover the logs. Additionally, temperature manipulation could be implemented using infrared lamps or heating cables placed inside the logs, similar to methods applied in soil experiments (e.g., Poll et al., 2013), to simulate future temperature scenarios. The study design would include a control treatment representing current climate conditions, along with two climate change scenarios (RCP 2.6 and RCP 8.5), both simulating increased temperatures and reduced precipitation (Figure 7).

Ongoing measurements of wood temperature and moisture would enable the quantification of environmental correlations, while systematic sampling of fungal mycelia and fruiting bodies could reveal species-specific patterns in survival, reproduction, and community dynamics under

altered climatic regimes. The experiment also provides an opportunity to investigate whether fungal fruiting body and spore traits adapt to specific temperature and moisture conditions, offering insights into the evolutionary adaptations, survival strategies, and dispersal dynamics of wood-inhabiting fungi. Continuous wood sampling would further allow for the assessment of decomposition dynamics across treatments, based on changes in lignin and cellulose content (e.g., Fravolini et al., 2018) (Figure 7).

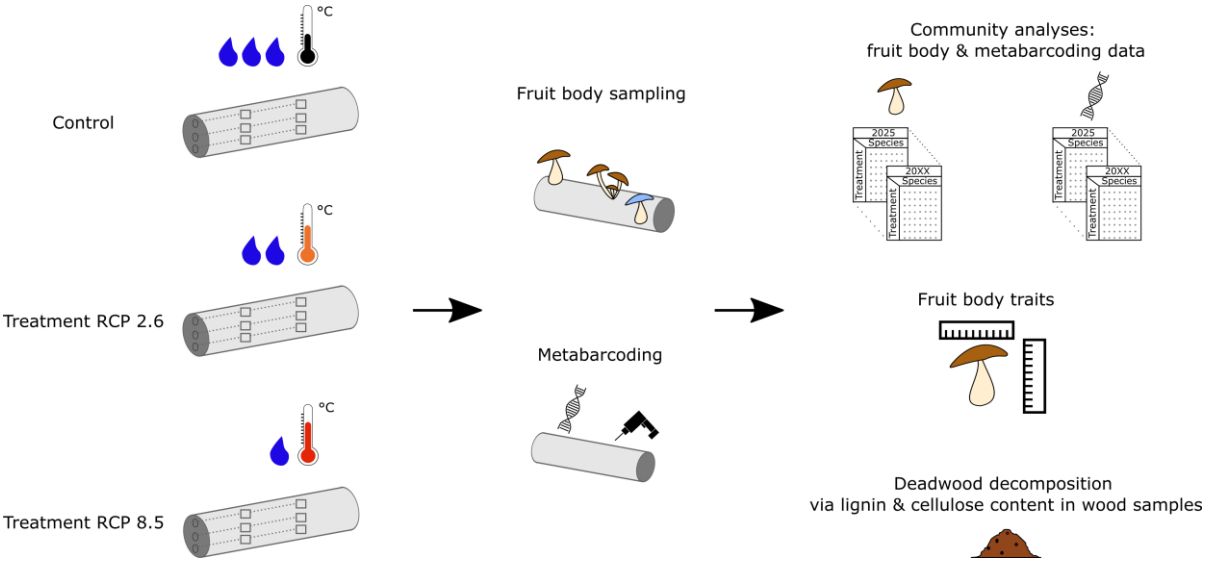

Figure 7: Conceptual study design to investigate the effects of increased temperature and reduced precipitation on fungal communities, assessed through both fruit body surveys and metabarcoding, as well as on deadwood decomposition and potential fruit body adaptations. Log moisture and temperature measurements are indicated by quadrates within the logs. Alongside current conditions (control), two climate change scenarios (RCP 2.6 and RCP 8.5) represent a gradient of warming and drying. Fungal data and wood samples would be collected from each treatment.

6 CONCLUSION

Deadwood plays a crucial role in forest ecosystems by providing habitats for diverse organisms and supporting essential ecological functions. Climate change, through increasing temperatures and increased disturbances such as windthrows, significantly affects these processes. However, knowledge gaps about how stand-scale and object-scale factors, which might occur after disturbances, affect deadwood decomposition processes still exist, making comprehensive predictions for future deadwood decomposition processes and associated ecosystem services difficult. Knowledge gaps remain because deadwood decomposition is a complex process influenced by various environmental factors and wood-inhabiting fungal diversity, which is also affected by the environment.

An overall important factor in biological processes is temperature and I could show, that canopy cover emerged as the primary driver of internal deadwood temperature. Open canopies increased mean and maximum temperatures during the growing season and decreased minimum temperatures in winter. Other factors, such as deadwood position, diameter, and surrounding deadwood amount, had weaker and less consistent effects. Thus, large-scale disturbances strongly affect internal deadwood temperature, which might have consequences on ecosystem functions and services provided by deadwood.

Furthermore, by using canopy cover as a proxy for microclimate, I analyzed long-term fungal fruiting body diversity and identified a (non-significant) successional pattern: fungal diversity initially increased but declined over time, with the decline being more pronounced under open canopies. Despite these changes, composition of fungal communities remained relatively stable, indicating resilience to projected shifts in canopy-mediated microclimatic conditions.

However, deadwood decomposition is a complex relationship between environmental factors and wood-inhabiting fungal diversity. To explore this, I simultaneously analyzed both the direct effects of the environment and the indirect effects via fungal diversity on deadwood decomposition. Decomposition was primarily influenced by tree species identity and canopy cover. Beech logs decomposed faster than fir logs, and decomposition was higher under open canopies. Although environmental factors affected fungal diversity, diversity contribution to decomposition was weak and inconsistent. This suggests that the carbon- and nutrient cycle in temperate forests is primarily affected by forest management decisions, such as tree species selection and logging intensity, which affect canopy cover. With increasing disturbances and more open canopies, a higher rate of deadwood turnover can be expected in the future.

These findings emphasize the importance of canopy cover in regulating deadwood processes and suggest that maintaining diverse canopy conditions can promote habitat heterogeneity and ecosystem resilience. However, knowledge gaps remain regarding object-scale microclimatic conditions, particularly the interaction between moisture and temperature and their effects on fungal diversity. Additionally, future research should investigate fungal functional traits across different microclimates and the long-term impacts of climate change on deadwood decomposition dynamics.

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8 AUTHOR CONTRIBUTIONS TO THE MANUSCRIPTS

The numbers shown in the table represent the authors' contributions to the manuscripts as percentages.

Manuscript 1: Effects of canopy-mediated microclimate and object characteristics on deadwood temperature, submitted to *Agricultural and Forest Meteorology*, 2024.

	Experimental concept & study design	Conduction of field and/or laboratory work	Evaluation of data & data analyses	Preparation of the manuscript
Jasper Schreiber	-	-	80	70
Václav Pouska	35	50	-	5
Petr Macek	35	50	-	5
Dominik Thom	-	-	5	5
Claus Bässler	35	-	15	15

The study concept was designed by CB, PM, and VP. PM and VP conducted the temperature measurements. JS primarily analyzed the data, with contributions to the analysis from CB and DT. JS drafted the initial manuscript. The revision and rewriting of the manuscript were carried out by JS, CB, VP, PM, and DT. JS is the corresponding first author.

Manuscript 2: Effects of experimental canopy openness on wood-inhabiting fungal fruiting diversity across succession, *Scientific Reports*, 2024.

	Experimental concept & study design	Evaluation of data & data analyses	Preparation of the manuscript
Jasper Schreiber	-	60	55
Petr Baldrian	20	-	-
Vendula Brabcová	-	-	5
Roland Brandl	20	-	-
Harald Kellner	-	-	5
Jörg Müller	30	-	-
Friederike Roy	-	-	5
Claus Bässler	30	10	10
Franz-Sebastian Krah	-	30	20

CB, JM, PB and RB designed the concept of the study. JS and FSK primarily analyzed the data, with contributions to the analysis from CB. JS and FSK interpreted the results and drafted the

initial manuscript with CB. VB, HK and FR helped with writing the final manuscript. JS is the corresponding first author.

Manuscript 3: Fungal fruit body assemblages are tougher in harsh microclimates, *Scientific Reports*, 2022.

	Experimental concept & study design	Evaluation of data & data analyses	Preparation of the manuscript
Franz-Sebastian Krah	50	70	65
Jonas Hagge	-	-	5
Jasper Schreiber	-	-	10
Roland Brandl	10	-	5
Jörg Müller	10	-	5
Claus Bässler	30	30	10

The study concept was designed by FSK and CB. CB, JM, RB designed the experimental setting of the study. FSK analyzed the data and wrote the first draft of the manuscript. CB contributed to data analysis, interpretation and writing of the manuscript. JS contributed to writing the manuscript. All authors critically revised the manuscript.

Manuscript 4: Unraveling the effect of environment and decomposer diversity on deadwood decomposition: Lessons from a large-scale experiment, *Ecological Processes*, 2025.

	Experimental concept & study design	Conduction of field and/or laboratory work	Evaluation of data & data analyses	Preparation of the manuscript
Jasper Schreiber	40	60	80	75
Friederike Roy	5	10	-	-
Harald Kellner	5	-	-	5
Vendula Brabcová	-	10	-	5
Petr Baldrian	20	-	-	5
Maximilian Stein	-	20	-	-
Claus Bässler	30	-	20	10

The study concept was designed by JS, CB, PB, HK and FR. JS and FR conducted the field work, VB, MS and JS conducted the laboratory work. JS primarily analyzed the data, with contributions to the analysis from CB. JS drafted the initial manuscript. The revision and

rewriting of the manuscript were carried out by JS, CB, HK and PB. JS is the corresponding first author.

9 LIST OF PUBLICATIONS

9.1 List of publications of this thesis

Schreiber, J.; Pouska, V.; Macek, P.; Thom, D.; Bässler, C. (2025a): Effects of canopy-mediated microclimate and object characteristics on deadwood temperature. *Agricultural and Forest Meteorology (362), 110378.*

Schreiber, J.; Baldrian, P.; Brabcová, V.; Brandl, R.; Kellner, H.; Müller, J.; Roy, F.; Bässler, C.; Krah, F.-S. (2024): Effects of experimental canopy openness on wood-inhabiting fungal fruiting diversity across succession. *Scientific Reports*, *14*(1), 16135.

Krah, F.-S.; Hagge, J.; **Schreiber, J.**; Brandl, R.; Müller, J.; Bässler, C. (2022): Fungal fruit body assemblages are tougher in harsh microclimates. Scientific Reports, 12 (1), pp. 1633.

Schreiber, J.; Roy, F.; Kellner, H.; Brabcová, V.; Baldrian, P.; Stein, M.; Bässler, C. (2025b): Unraveling the effect of environmental and fungal diversity on deadwood decomposition: Lessons from a large-scale experiment. *Ecological Processes, 14(1), 1-17.*

9.2 Further publications

Oechler, H.; Krah, F.-S.; **Schreiber, J.**; Baldrian, P.; Brabcová, V.; Kellner, H.; Roy, F.; Bässler, C. (2025): Disentangling effects of structural deadwood characteristics on fungal and bacterial diversity and assembly. *Under review in Conservation Biology*.

Roy, F., Ibayev, O., Arnstadt, T., Bässler, C., Borken, W., Groß, C., Hoppe, B.; Hossen, S.; Kahl, T.; Moll, J.; Noll, M.; Purahong, W.; **Schreiber, J.**; Weisser, W.; Hofrichter; M.; Kellner, H. (2023). Nitrogen addition increases mass loss of gymnosperm but not of angiosperm deadwood without changing microbial communities. *Science of the Total Environment*, 900, S. 165868.

Non-peer-reviewed article:

Schreiber, J. (2022): Invasive Herbivoren auf ozeanischen Inseln und deren Auswirkungen auf bedrohte Pflanzenarten. In: Treffpunkt Biologische Vielfalt – Jubiläumsband. 20 Jahre interdisziplinäre Forschungsaustausch im Rahmen des Übereinkommens über die biologische Vielfalt. Schliep, R.; Stadler, J. (Hg.). Bundesamt für Naturschutz (BfN-Schriften, 632). Bonn.

10 MANUSCRIPTS

10.1 Effects of canopy-mediated microclimate and object characteristics on deadwood temperature

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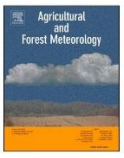

Effects of canopy-mediated microclimate and object characteristics on deadwood temperature

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ABSTRACT

Deadwood is a crucial component of forest ecosystems, supporting numerous forest-dwelling species and ecosystem functions, such as water and nutrient cycling. Temperature is a major driver of processes, affecting, *inter alia*, metabolic rates within deadwood. Deadwood temperature is determined by factors at both the forest stand-scale and individual deadwood object-scale. Yet, the contribution of individual factors within the complex hierarchy of scales that drive temperature in deadwood remains poorly understood. We conducted a real-world experiment to analyze the effects of forest stand canopy cover (open vs. closed canopies), surrounding deadwood amount (high vs. low), deadwood tree species (beech vs. fir), position (soil contact vs. uplifted) and diameter (range: 19-47 cm) of coarse woody debris on within-deadwood daily mean, minimum and maximum temperature at monthly and seasonal level. Stand-scale factors were more important than object-scale factors for explaining the variance in temperature. Canopy cover exhibited the strongest relationship with temperature. Daily mean and maximum temperature were higher and daily minimum temperature was lower in open than in closed canopies during the growing season (May-October). Further, daily minimum was lower in open canopies during winter (November-April). Annual daily mean and maximum temperature were about 1 °C and 5 °C warmer, respectively, and minimum temperature about 2 °C colder in open compared to closed canopies. Effects of deadwood amount, object diameter, position, and tree species on temperature were less important and statistically significant in only a few months. We conclude that canopy cover is more important than deadwood characteristics in determining internal deadwood temperature. An increase of canopy disturbance will hence elevate the temperature in deadwood, which might have important consequences on deadwood-dwelling species and ecological processes, such as heterotrophic respiration. To diversify habitat conditions for multiple species, we recommend enriching deadwood under various canopy conditions.

1. Introduction

Deadwood is an important component of all forest ecosystems globally. It contributes substantially to global forest biodiversity and functioning, and hence to crucial ecosystem services like the provisioning of wood, ecosystem regulation, cultural services, and habitat maintenance (Eräjää et al., 2010; Janeczko et al., 2021; Kuehne et al., 2008). However, deadwood amount, heterogeneity and the related ecological processes and services are heavily affected by global climate change, both directly (e.g., via temperature increase) and

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indirectly (e.g., via climate-induced disturbances) (e.g., Seidl et al., 2014; Seidl et al., 2017).

Temperature is among the most important predictor for biological processes in deadwood, as it directly influences mechanisms like thermoregulation. The most influential organisms driving deadwood decomposition are ectotherms (e.g., fungi, bacteria, insects), i.e., organisms regulating their body temperature primarily through external thermal conditions. Temperature in deadwood determines the thermal niche of ectotherms and hence the community composition of organisms in deadwood (Lennon et al., 2012; Maynard et al., 2019). A second mechanism is metabolic rate, that is the rate at which an organism converts chemical energy stored in food sources into usable energy. For example, metabolic processes like enzymatic activity to decompose deadwood depend strongly on temperature (Magan, 2008). As temperature increases, decomposition rates might accelerate due to increased metabolic activities of deadwood-dwelling organisms (Forrester et al., 2012). Consequently, the release of carbon driven by heterotrophic respiration is expected to increase (Forrester et al., 2012; Herrmann and Bauhus, 2013; Rinne-Garmston et al., 2019). On the other hand, warmer temperatures might lead to a loss of less warm-tolerant species (due to their physiological constraints), which ultimately affects the deadwood-dwelling community. This might have consequences on related ecosystem processes like decomposition (Barbé et al., 2020; Maynard et al., 2019). Yet, the manifold factors driving temperature in deadwood are unknown, hindering the prediction of cascading effects from altered ectothermic activity over decomposition rates to ecosystem processes (e.g., carbon- and nutrient-cycling) under climate change.

Temperature in a deadwood object might be affected by different factors acting at different scales. At stand scale, canopy cover strongly influences microclimate conditions in forests (e.g. Thom et al., 2020; Zellweger et al., 2020). However, the buffering capacity of canopy cover depends on temporal fluctuations in macroclimatic conditions and on local stand and site conditions (Rita et al., 2021; Thom et al., 2020). Studies focusing on temperature in deadwood under various canopy conditions across years are scarce. However, it was recently shown that temperature inside deadwood was higher under open compared to closed canopies (Lindman et al., 2022; Romo et al., 2019). For example, during the summer months, the average maximum temperature in pine deadwood located in clear-cut areas was approximately 5-6 °C higher than in deadwood within pine stands in New Zealand (Romo et al., 2019). This indicates that climate change not only increases temperature directly, but also indirectly by boosting canopy disturbance caused by multiple disturbance agents (e.g., windthrow, insect calamities) (Schmidt et al., 2017; Seidl et al., 2017; Senf and Seidl, 2021), reducing the microclimatic buffering capacity of forest ecosystems. Consequently, the effects of climate change on the thermal conditions inside deadwood are twofold: direct via atmospheric warming, and indirect via increased canopy openness. A first step towards a better understanding of what this means for ecosystem processes, is to analyze the temperature inside deadwood under various canopy conditions.

The amount of deadwood in a forest stand might also affect the temperature within a deadwood object. With an increasing amount of deadwood in a forest stand, the temperature of a deadwood object might increase due to a higher temperature absorption of the surrounding objects (i.e., lower albedo) (Cherubini et al., 2012). For example, snowmelt studies showed that due to the increasing absorption of solar radiation of deadwood via the black body effect, the nearby temperature increases and elevates snowmelt rates (Marangon et al., 2022). Further, Cherubini et al. (2012) suggested that albedo increased with the removal of organic material in forest ecosystems. However, other studies at stand-scale did not detect a notable effect of deadwood on the forest microclimate (Kovács et al., 2017; Thom et al., 2020). It remains unclear whether surrounding deadwood affects temperature inside deadwood, potentially resulting in alterations of processes inside deadwood. Further, it is unclear whether a critical amount and a specific arrangement (e.g., clustered versus distributed) of deadwood changes internal deadwood temperatures.

Several factors at the scale of an individual deadwood object might further influence temperature within deadwood. (i) The diameter of the deadwood object: Previous studies indicated that the average minimum temperature of logs increased from object surface to object center while, at the same time, temperatures were less variable (Romo et al., 2019, Walczyńska and Kapusta, 2017). In effect, temperature stabilizes with increasing deadwood diameter (Pouska, et al., 2016). Yet, the role of diameter on deadwood temperature remains unclear when accounting for other confounding factors. (ii) The position of the deadwood object: Lindman et al. (2022) found that the mean temperature inside deadwood was higher in standing compared to downed deadwood indicating differences in the exposition to radiation (Hutchison and Matt, 1977). However, soil contact may also increase deadwood moisture and thus latent heat, inducing a local cooling effect (e.g., Pouska, et al., 2016). Further, downed and standing deadwood objects often differ in decay stage, altering the capacity to store water within deadwood with potential consequences on temperature (Uhl et al., 2022). Thus, the extent of soil contact of a deadwood object might critically affect within deadwood temperatures. (iii) Wood chemical- and physical characteristics (e.g., wood density, Paletto and Tosi, 2010) differ substantially among tree species: An important event in evolution causing significant differences in chemical and physical properties was the split between Angio- and Gymnosperm tree species (Lombardi et al., 2013; Pietsch et al., 2014; Weedon et al., 2009). To the best of our knowledge only few studies measured temperature inside deadwood, but they did not distinguish among tree species (Graham, 1925; Lindman et al., 2022; Pouska, et al., 2016; Pouska et al., 2017; Romo et al., 2019; Savely, 1939; Walczyńska and Kapusta, 2017). Thus, it remains unknown whether tree species with different physico-chemical properties also have different temperatures under similar environmental conditions.

Here, we conducted a real-world manipulation experiment at both the stand-scale and the deadwood-object scale to unravel the contribution of hierarchical factors on the internal temperature of deadwood. We compiled a unique dataset to derive the importance of individual drivers on daily mean, minimum, and maximum temperatures inside deadwood.

2. Material and methods

2.1. Study area and study design

The within deadwood temperature measurements were conducted in a long-term deadwood experiment in the management zone of the Bavarian Forest National Park in southeastern Germany (48°540N, 13°290E). The management zone is characterized by mixed mountain forests, dominated by Norway Spruce (*Picea abies* (L.) H. Karst), European Beech (*Fagus sylvatica* L.) and Silver Fir (*Abies alba* Mill.) (Bässler et al., 2011). Mean annual temperature (1972-2001) and total annual precipitation varies depending on altitude between 3.5 °C to 7.0 °C and 1300 mm to 1900 mm, respectively (Bässler et al., 2010). A biodiversity survey in the study area revealed that the main growing season with most species activity is roughly between May and October (Bässler, et al., 2015). This is also the period with the highest activity of deadwood-depending species on beetles and fungi (Krah et al., 2018; Lettenmaier et al., 2022; Seibold et al., 2016).

Twelve plots with a standardized size of 0.1 ha were established in four different sites (blocks) across the study area (ca. 48 km^2, minimum distance between sites: 2.4 km). Half of the plots were characterized by closed and the other half by open canopies. Plots contain either low (25.20 m^3/ha on average) or high (178.12 m^3/ha on average) amounts of deadwood. Deadwood was harvested with chainsaws from stands with similar conditions (elevation, age, tree species composition, etc.) and brought to the plots at the end of 2011 (Table S1, see more in-depth description of the experiment in Krah et al., 2018). Three to five beech and/or fir deadwood objects (diameter range: 19-47 cm; average

diameter: 32 cm; length: 5 m) were randomly selected on each plot to balance the number of objects across our plots. The objects were either completely lying on the ground or uplifted (stacked over other objects with < 50 % soil contact). Altogether, the experiment included 26 objects in open and 24 objects in closed canopies, of which 25 were beech and 25 fir objects, 23 of which were uplifted and 27 were with complete soil contact (Table S1). Note that the design is unbalanced for the predictor deadwood amount with 10 objects characterized by low and 40 objects by high amounts of deadwood. We account for this imbalance in our analyses (i.e., test for heteroscedasticity; for more details, see section data preparation and statistical analyses). Our factorial predictors were canopy cover (open versus closed), deadwood amount (high versus low) position (lying versus uplifted) and tree species (beech versus fir). As we have measured the deadwood amount (m^3/ha) on each plot and because there is a high variability of deadwood amount within the categories (high and low amount), we considered this predictor as a continuous variable (Table S1). However, note that the results are robust if considering deadwood amount as a factor in the models (data not shown). Therefore, the final continuous predictors were deadwood amount and object diameter.

Inside the 50 deadwood objects, temperature was recorded at 15-minute intervals from May 19th, 2016, to October 31st, 2019, in the wood sub-surface layer using Pt100 resistance thermometers connected to data loggers (MINILOG-T6, Fiedler AMS, České Budějovice, Czech Republic). In each object, one thermometer was inserted at the cross-section of the object, 5 cm below the object surface and 10 cm deep inside the object. This allows a comparison with other studies and further, temperature measures at this depth were significantly related to saproxylic diversity (Pouska, et al., 2016; Pouska et al., 2017). The thermometers of uplifted objects were inserted at their upper ends. At each thermometer the object diameter was measured (Fig. 1).

2.2. Data preparation and statistical analyses

First, we harmonized the collected data and removed potential unrealistic values. To determine potential unrealistic values, we used temperature data from a nearby meteorological station (Waldhäuser). In the months of December to March, we removed all values above 20 °C, values below –20 °C and values that showed a deviation of +/- 10 °C from the meteorological station. In the months of April to September, we removed all values that showed a deviation of +/- 20 °C. We consider this procedure as a conservative approach. However, >99 % of the data

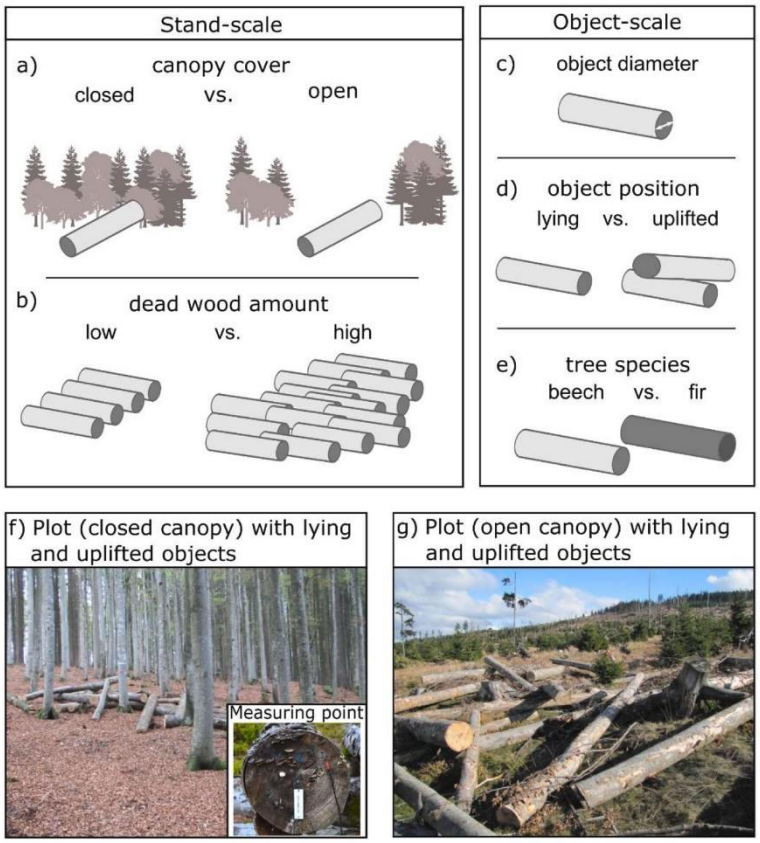

Fig. 1. Experimental deadwood temperature setup (a-e): Stand-scale factors are (a) canopy cover and (b) deadwood amount in the immediate surrounding (within the plot). Deadwood-object scale factors are (c) diameter, (d) position, (e) tree species. Illustration of plot and object conditions (f, g): Left (f); plot under closed canopy conditions with high amount of deadwood and lying and uplifted objects. The inset in (f) shows the position of the thermometer (inserted at the cross-section of the object, 5 cm below the object surface and 10 cm deep inside the object). Right (g); plot under open canopy conditions with a high amount of deadwood and lying and uplifted objects.

points remained after this cleaning step and we, therefore, safely assume that this reduction should not have substantial effects on the study's inferences. Second, we calculated the daily mean, minimum and maximum temperature from the cleaned 15-minute values. Third, based on these data, we identified thermometers that were most likely covered with snow during wintertime. Snow days were defined based on the assumption that within a three-day time window the daily maximum temperature and the difference between daily maximum and daily minimum temperature remain relatively constant or do not exceed a certain threshold: the thresholds for the three-day window for the difference in daily maximum temperature was set to 1.25 °C and the temperature variation within a day should not exceed 1 °C. These thresholds were adapted from the 'myClim' package in R (Man et al., 2023). All detected snow days were compared to the snow level data from the nearby meteorological stations Waldhäuser and Großer Rachel and were finally removed, if the stations confirmed the existence of snow. Due to the high number of snow days in all sample years, the month January was omitted from the analyses. Due to this procedure and temporary failure of some data loggers, we could use the data from June-December in 2016, February-November in 2017, February-December in 2018 and March-October in 2019 (Table S2).

We applied multivariate linear mixed effect models to test simultaneously the influence of stand-scale variables (canopy openness, deadwood amount) and object characteristics (diameter, position, tree species) on the mean, minimum and maximum temperature inside deadwood based on daily data on monthly and seasonal level. We used the function *lme* within the R package 'nlme' (Pinheiro and Bates, 2000). We defined the seasons as (i) the period with most of the species' activity in the study area based on biodiversity survey data (May-October, Bässler et al. (2015), see also above) versus winter time (November--April) and (ii) meteorologically for our locality to allow comparison with similar studies (Deutscher Wetterdienst, 2024). Meteorological seasons were defined as spring (1^{st} of March – 31^{st} of May), summer (1^{st} of June – 31^{st} of August), autumn (1^{st} of September – 30^{th} of November) and winter (1^{st} of December - $28/29^{th}$ of February). To account for the influence of the macroclimate conditions of the respective years in the models, the mean annual temperature of the respective years (2016-2019) from the nearby meteorological station Waldhäuser was included as a covariate (Fig. S1). The continuous explanatory variables (deadwood amount and object diameter) were standardized (z-transformed). All response variables were normally distributed and collinearity among predictors was low ($r<|0.04|$). Levene tests revealed low levels of heteroscedasticity for the predictors. To account for the nested structure within our study design, we included a nested random effect, that is, plot within site. As consecutive temperature measurements might result in temporal autocorrelation, we included the first order autocorrelation, using the function *corAR1* within the R package 'nlme' in our models. We used the Durbin-Watson statistics (function *DurbinWatsonTest* within the R package 'DescTools' (Signorelli and et mult. al., 2021)) to evaluate whether the autocorrelation term within the model reduced temporal autocorrelation. For the interpretation of the results, we used the descriptive plots based on the raw values (Fig. S2-S7) and the full model output (estimate, SD, t-value, p-value). We report the t-values of the model (predictor estimate divided by SD, a type of signal-to-noise-ratio) to provide a direct comparison of the effects among predictors while considering the variability in the data. We also derived the marginal R^2 that represents the explained variance by the fixed effects, using the function *r.squaredGLMM* within the 'MuMIn' R package (Barton, 2024).

The Durbin-Watson statistic revealed significant ($p<0.05$) mean values between 0.24 and 0.92 for our models, and hence, still indicated weak temporal autocorrelation (Draper and Smith, 1998; Durbin and Watson, 1950). For this reason, we applied additional models using mean temperature values aggregated for each month as response variable. For these data, we set a threshold for daily data missing within a month to avoid aggregation bias. Specifically, we adopted the "5/3 rule" for data completeness suggested by the World Meteorological Organization (Anderson and Gough, 2018). This rule states that no more than five missing daily values or no more than three consecutive missing daily values should occur in a month (World Meteorological Organization, 2017). Following this convention, we calculated the monthly average of daily mean, minimum and maximum temperature for each object. As a result, data from a different number of objects were available for analysis of each month of the year (Table S2). Monthly linear mixed effect models were applied using the function *lmer* within the R package 'lme4' (Bates et al., 2015) using annual temperature in the offset argument to account for the annual difference in mean temperature, and we used plot nested within site as random effect. This exercise demonstrated that the inferences drawn from the daily models with weak temporal autocorrelation are overall robust (Table 1, Table S3). However, in order to reduce the potential bias in the interpretation of the model with daily resolution, we report the results of both model approaches. Furthermore, our monthly data span multiple years, but we do not have complete data for every month in each year. Although the mean annual temperature for the respective years was included in our overall models, this variation in data availability could introduce bias. To address this, we also modeled each month of each year separately, based on the available data. This exercise supported the findings of the overall models (data not shown), and we therefore present the models for each month and season, incorporating all available data across the years.

3. Results

3.1. Deadwood temperature

We observed a pronounced temporal variation in temperature inside deadwood. The highest measured mean daily temperature was 31.42 °C (August 2017) and the lowest -10.12 °C (February 2018, Fig. S2). During these months, the lowest daily minimum temperature (-17.31 °C in February 2018) and the highest maximum temperature (49.65 °C in August 2017) were also measured (Fig. S2). Over the winter seasons (November-April, excluding January, see method section), the measured daily mean temperature was 5.29 °C, the minimum temperature was 2.20 °C and the maximum temperature was 8.38 °C. The average daily temperatures in the growing seasons (May-October) were up to ~9 °C higher than in the winter seasons, with a measured daily mean temperature of 14.23 °C, a minimum temperature of 10.52 °C and a maximum temperature of 17.95 °C.

3.2. Deadwood temperature drivers per month

3.2.1. Daily mean temperature

Our models reveal that canopy cover has the strongest effect on deadwood daily mean temperature (Table 1). In June, July and August, the mean deadwood temperature was significantly higher in open compared to closed canopies (Table 1 and Fig. 2). On average, daily mean temperature was 2 °C warmer in open than in closed canopies during these months (Fig. 2). The month with the largest difference among canopy treatments was June (2.35 °C). In contrast, in October and December, the mean deadwood temperature was significantly lower in open than in closed canopies (Table 1 and Fig. 2). Furthermore, the daily mean temperature was negatively affected by deadwood amount in June and July (Table 1). However, this was not supported by the models based on monthly aggregated data (Table S3, used as sensitivity analysis to account for temporal autocorrelation observed in the models based on daily resolution, see statistical analysis). Finally, fir deadwood was characterized by significantly lower daily mean temperature than beech deadwood in June, July and August (Table 1). On average, daily mean temperature was by 0.96 °C lower in fir than in beech deadwood during these months (Fig. 2). However, the difference in June was not significant in the monthly aggregated model (Table S3).

Table 1
T-values (predictor estimate divided by SD) of the monthly and seasonal models testing stand and object scale variables on deadwood mean, minimum and maximum temperature. A positive t-value indicates higher temperature values in the reference group (open canopy, uplifted position, fir deadwood) or an increase in temperature with increasing deadwood amount and object diameter (see method section). Conversely, a negative t-value indicates lower temperature values in the reference group or a decrease in temperature with increasing deadwood amount and object diameter. Values in bold represent significant effects. Significance levels are *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$. For exact p-values and full model outputs see Table S5. The marginal R^2 represents the explained variance by the fixed effects (stand and object scale variables) in each model. Models are based on the years 2016-2019. Growing season versus winter were defined based on biological data of the study area (see method section). Note that January is not shown due unreliable data caused by high numbers of days with snow cover.

		Canopy (reference "open")			Deadwood amount			Object diameter			Position (reference "uplifted")			Tree species (reference "fir")			Marginal R^2		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Month	2	-1.95	**-2.49***	-1.25	1.06	1.9	-0.21	-0.77	-0.74	-0.74	-0.39	-1.37	1.32	-0.79	-1.2	-0.09	*0.14*	*0.20*	*0.06*
	3	-1.34	**-3.88****	-0.12	-0.82	-0.54	-1.29	0.9	-0.25	0.75	0.86	-0.24	0.88	-0.56	-1.42	-0.44	*0.36*	*0.25*	*0.35*
	4	-0.03	**-8.36*****	1.35	-0.14	-1.3	-0.92	1.31	0.71	-0.3	1.39	0.88	0.5	-0.98	-0.91	-0.48	*0.02*	*0.22*	*0.03*
	5	1.01	**-2.87***	**4.12****	-0.77	-0.37	-0.27	0.55	0.98	-0.17	0.89	0.88	0.64	-1.24	-0.94	-1.44	*0.28*	*0.29*	*0.24*
	6	**6.98*****	**-3.94****	**4.39****	**-3.68****	-0.4	-0.21	0.1	1.41	-0.44	1.8	0.36	1.31	**-2.66****	-0.8	-1.42	*0.14*	*0.23*	*0.25*
	7	**4.12****	**-3.57***	**4.24****	**-2.68***	-0.28	-0.03	-0.18	0.89	-0.55	1.27	0.09	0.52	**-2.45***	-1.17	-1.81	*0.18*	*0.24*	*0.30*
	8	**2.66***	**-5.12****	**3.72*****	-0.99	-0.39	0	0.02	1.36	-0.87	0.58	-0.09	0.79	**-2.17***	-1.65	**-2.03***	*0.13*	*0.25*	*0.27*
	9	0.52	**-9.93*****	**8.02*****	-0.09	-0.35	-2.22	0.81	1.4	-0.34	0.05	-0.6	0.56	-0.92	-0.52	-1.73	*0.05*	*0.16*	*0.18*
	10	**-2.51***	**-4.33****	0.4	0.15	-0.04	-1.25	**2.14***	0.36	-0.81	0.92	-0.47	0.64	-1.01	-1.06	-0.94	*0.16*	*0.23*	*0.12*
	11	-1.49	**-5.07****	0	-0.42	-0.18	-0.68	0.32	0.26	0.55	0.26	-0.59	0.95	-0.09	-0.35	-0.08	*0.37*	*0.31*	*0.36*
	12	**-3.24***	-2.33	**-2.67***	-0.04	1.16	-1.3	-0.62	-1	-0.1	-1.1	-1.59	-0.29	-0.09	-1.45	0.93	*0.08*	*0.12*	*0.05*
Season	Winter	0.3	**-7.73*****	**2.91***	-0.75	0.73	-0.91	-0.17	0.11	-0.33	-0.55	-1.35	-0.5	-1.18	-1.78	-0.65	*0.06*	*0.14*	*0.07*
	Nov-Apr																		
	Growing season May-Oct	**6.57*****	**-9.87*****	**20.47*****	-1.92	-0.79	**-3.83****	-0.34	1.37	-1.74	0.71	-0.31	1.95	**-2.29***	-1.13	**-4.09*****	*0.11*	*0.12*	*0.17*

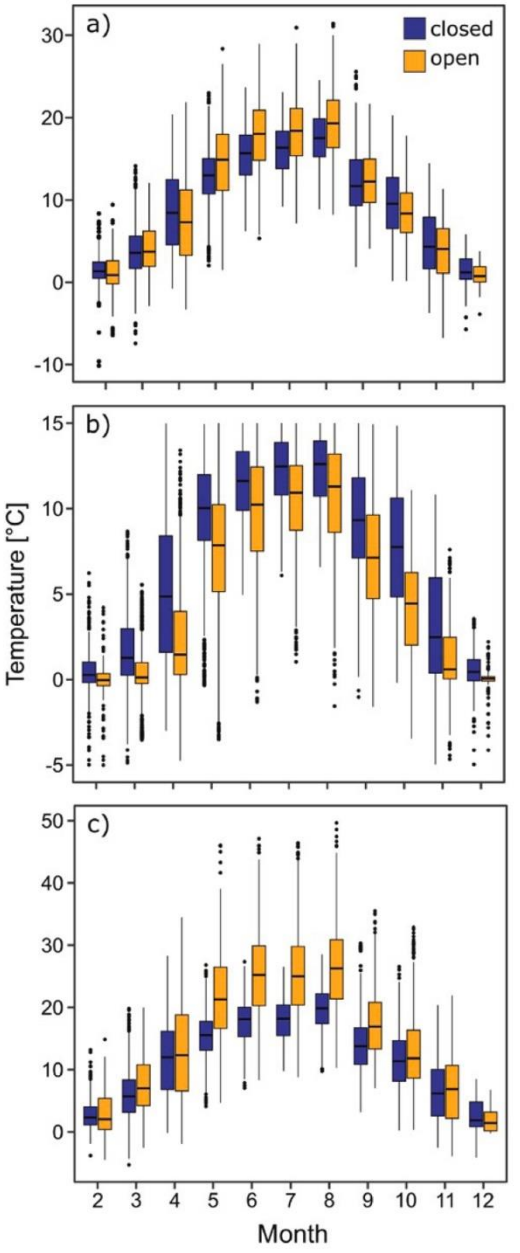

Fig. 2. Boxplots of daily a) mean, b) minimum and c) maximum temperatures inside deadwood from open and closed canopies in each month of 2017 and 2018 (most complete data). Note that in December, only values from 2018 are presented due to missing data in 2017. January is not shown due to unreliable data caused by high numbers of days with snow cover.

3.2.2. Daily minimum temperature

Our models revealed that the daily minimum temperature was significantly lower in open canopies from February to November (Table 1). However, effects were not significant in February, March and May in the monthly aggregated models (Table S3). On average, daily minimum temperature was 2.08 °C colder in open than in closed canopies during from February to November (Fig. 2). The month with the largest difference was October (-3.31 °C). The amount of surrounding deadwood, object diameter, object position or tree species had no significant influence on the daily minimum temperature in any month (Table 1, Table S3).

3.2.3. Daily maximum temperature

The daily maximum temperature was significantly higher in open canopies from May to September and significantly lower in open canopies in December (Table 1, Tab S3). On average, daily maximum temperature was 6.39 °C warmer in open than in closed canopies during May to September (Fig. 2). The month with the strongest difference was June (7.60 °C). Furthermore, maximum daily temperature was significantly lower in fir than in beech deadwood in August (Table 1), however, this was not supported by the models based on monthly aggregated data (Table S3).

3.3. Deadwood temperature drivers per season

The growing season in our study is defined from May-October and the winter season from November-April (see data preparation for explanation). The presented results for the growing and winter season are similar to the model results based on meteorologically defined seasons (spring, summer, autumn, winter, see data preparation for definition and Table S4 for the results).

3.3.1. Daily mean temperature

We found no significant effects of any variable explaining daily mean temperature of the winter season (Table 1). In contrast, daily mean temperature was significantly higher in open than in closed canopies in the growing season (Table 1 and Fig. 3). On average, daily mean temperature was 1.12 °C warmer in open than in closed canopies in the growing season (Fig. 2). Further, daily mean temperature was lower in fir than in beech deadwood in the growing season (Table 1).

3.3.2. Daily minimum temperature

The daily minimum temperature of both the winter and growing seasons was significantly lower in open than in closed canopies (Table 1 and Fig. 3). On average, daily minimum temperature was -1.80 °C colder in open than in closed canopies in the winter and -2.81 °C colder in the growing season (Fig. 2). No other treatments had a significant effect on daily minimum temperatures.

3.3.3. Daily maximum temperature

The daily maximum temperature showed significantly higher values in open canopies in both winter and growing seasons, however, the effect was stronger in the growing season (Table 1 and Fig. 3). On average, daily maximum temperature was 1.87 °C warmer in open than in closed canopies in the winter and 5.05 °C warmer in the growing season (Fig. 2). The daily maximum temperature of the deadwood was significantly lower on plots with high amount of surrounding deadwood and in fir deadwood in the growing season (Table 1, and Fig. 3).

4. Discussion

Across all months and seasons, we found that temperature in deadwood is mainly driven by canopy cover. Open canopies exhibited greater variation in microclimates with lower minimum temperatures throughout the year and higher mean and maximum temperatures during the growing season. In comparison, deadwood amount at stand-scale and the object-scale factors diameter, position and tree species were of lower importance for mean, minimum and maximum temperature variability in deadwood.

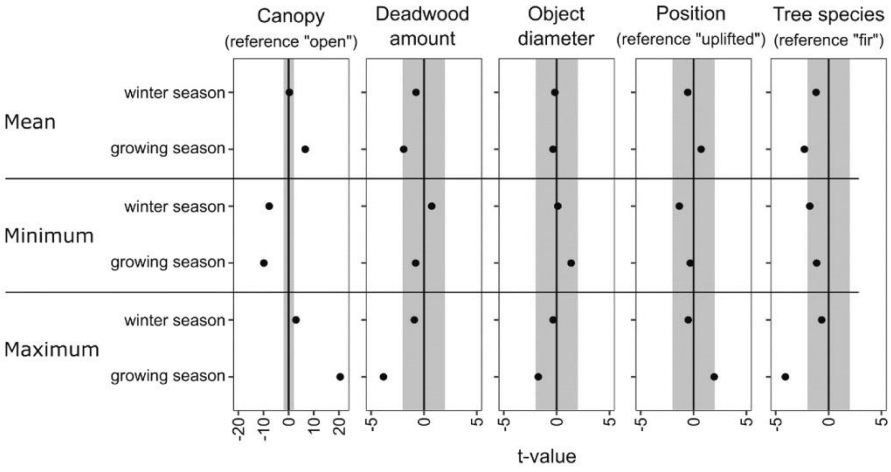

Fig. 3. T-values (predictor estimate divided by SD) from the seasonal models testing stand and object scale variables on deadwood daily mean, minimum and maximum temperature. A positive t-value indicates higher temperature values in the reference group (open canopy, uplifted position, fir deadwood) or an increase in temperature with increasing deadwood amount and object diameter (see method section). Conversely, a negative t-value indicates lower temperature values in the reference group or a decrease in temperature with increasing deadwood amount and object diameter. Models are based on the years 2016-2019. Growing season (May-October) versus winter (November-April, without January) is defined from biological data of the study area (see method section). Shaded areas indicate the range of non-significant values (95 % confidence level, see also Table 1). Note that the x-axes differ among the predictor variable canopy cover and the other predictor variables.

4.1. Strong effect of canopy cover on deadwood temperature

We found that maximum temperature was significantly higher and minimum temperature was significantly lower in open canopies in the growing season (May-October). The observed effects of canopy openness on the within object temperatures can be explained by the buffering capacity of temperatures by closed canopy (De Frenne et al., 2019; Thom et al., 2020; Zellweger et al., 2020). Intact forest canopies shelter the ground from solar radiation (Graham, 1925; Lindman et al., 2022). In addition, evapotranspiration increases with hotter and drier weather conditions during the growing season, compensating weather extremes to some degree (Thom et al., 2020). Therefore, our results support the view that canopy cover buffers microclimate extremes and that these effects are stronger in summer during the leaf-on phase than in winter in the leaf -off phase (Zellweger et al., 2019). However, our models revealed also that the daily minimum temperature is significantly lower in open conditions in winter. This indicates a clear buffering of extreme minimum temperatures by closed canopies even outside the growing season.

The strong relationship between deadwood temperature and canopy cover allows inferences and predictions about consequences on the diversity and decomposition processes in times of climate change. We expect that deadwood in our forests will experience higher temperatures in future. Basically, higher temperatures can increase heterotrophic respiration and thus wood decomposition rates (Forrester et al., 2012; Herrmann and Bauhus, 2013; Mackensen, et al., 2003; Russell et al., 2014; Seibold et al., 2021). However, higher average temperatures and more open canopy conditions might result in novel extreme temperature conditions exceeding the physiological tolerance of deadwood organisms (Maynard et al., 2019; Stokland et al., 2012). This might have consequences on the species diversity patterns in deadwood but also on the related ecosystem processes (e.g., decomposition) via metabolic constraints. On the other hand, previous studies found evidence that the community composition of species that substantially contribute to the decomposition of deadwood (fungi and beetles) differ between open and closed canopies under current conditions (Krah et al., 2018; Seibold et al., 2016). This indicates that different deadwood decomposer communities are associated with different microclimate conditions (Boddy and Heilmann-Clausen, 2008; Fukasawa, 2021). Thus, if moisture is not limiting, decomposition rates might increase in future and hence boost the carbon and nutrient cycle in temperate forest (Crockatt and Bebber, 2015; Eichenberg et al., 2017). However, moisture might become a limiting factor in future and hence, decomposition rates might decrease (Oberle et al., 2018; Seibold et al., 2021).

4.2. Limited effects of deadwood amount, diameter, position and tree species on deadwood temperature

Variables aside from canopy cover had minimal impact on deadwood temperature. The amount of deadwood in our models showed weak negative effects on object mean temperature in June and July (Table 1) while the monthly models based on aggregated daily values did not indicate any effect of the amount of deadwood on mean temperature (Table S3). This contradicts our expectation that a higher deadwood amount would lead to a higher temperature in an object due to lower albedo and higher water storage (Cherubini et al., 2012). We are aware that sample size for the predictor deadwood amount was unbalanced in our setting. However, since heteroscedasticity in our models was low, we conclude that the effect of deadwood amount on deadwood temperature is negligible at the scale of our study. This is in line with findings of Klicken oder tippen Sie hier, um Text einzugeben.Thom et al. (2020)Klicken oder tippen Sie hier, um Text einzugeben., Klicken oder tippen Sie hier, um Text einzugeben.Haughian and Frego (2017) and Kovács et al. (2017), who could not identify any impact of deadwood on surrounding air temperature of the forest stand. Further studies are needed that disentangle potential thermal absorbing effects of various amounts of deadwood relative to other factors which might affect forest microclimate conditions at stand scale, such as understory vegetation and soil structure (e.g. soil color).

The diameter of deadwood objects had also only minor effects on internal deadwood temperature. We expected that a larger object would be characterized by greater thermal inertia, which would result in different temperatures depending on the diameter of the object. We found only a non-significant tendency for slightly higher medians of the minimum temperature in larger diameter objects in the growing season based on the plotted raw values without controlling for other confounding factors (Fig. S5). One explanation for the weak effects, we observed could be that only deadwood with generally larger diameter (coarse woody debris) was considered in our study. Even though the diameter of our objects varied considerably (19-47 cm), most objects had >30cm in diameter (>65 %). In the study by Pouska, et al. (2016), who found that temperature stability increased with diameter, the range of diameter was 10-103 cm. Therefore, variability of diameters among our studied objects might be too low to reveal significant effects. Further, temperature in our study was consistently measured at a standard distance of 5 cm below the object surface, specifically at the cross-section end. Measures at this standard depth might have received a stronger influence of the surrounding air temperature on within-deadwood temperature far overlaying effects of diameter variability. Indeed, Walczyńska and Kapusta (2017) found that the minimum temperature inside stumps increased with horizontal depth, while temperature variation decreased during winter. This indicates that the depth of measurement is crucial for determining the deadwood objects' temperature buffering capacity in relation to the environment. More studies are needed in which temperature sensors should be set up at different positions and depth in deadwood while considering a broad range of diameter classes and environmental conditions.

Across our models, we found no support that uplifted objects have significantly higher temperatures than objects lying on the ground, even though the raw data indicated some differences (Fig. S6). This contrasts with the study by Lindman et al. (2022) who demonstrated that standing deadwood (snags) was warmer than lying deadwood. The different results might be explained by the exposure to radiation, that is, a complete vertical position in the study by Lindman et al. (2022) versus still horizontally oriented uplifted position in our study. Furthermore, Lindmann et al. (2022) reported that downed logs can be covered by near-ground vegetation which protects them from direct sunlight. In our setting, we experimentally standardized our plots which did not lead to a difference in vegetation cover between lying and uplifted objects. Thus, sunlight reached lying and uplifted objects in a similar way, which might also explain these contrasting results.

Temperatures were significantly lower in fir than in beech deadwood during warmer months (July, August) and in the growing season respectively meteorological summer (Table 1, Table S3,4). As we have not measured physical properties or other object characteristics like deadwood surface structure (e.g., bark cover and color), we can only speculate about the observed differences. One explanation could be the different physical properties of Angio- and Gymnosperms (Weedon et al., 2009). In general, fir wood is less dense than beech wood (Petritan et al., 2023). As density affects the thermal conductivity (Suleiman et al., 1999), the lower density of fir deadwood might absorb and store less heat than the denser beech deadwood. Furthermore, the color (i.e., lightness) of bark and wood (if partly or completely debarked, e.g., due to decomposition) can vary between tree species and thus determine the absorption of thermal energy via differences in albedo. The color of wood might also be affected by the fungal communities that colonized the deadwood. For example, white rot fungi produce light colors as cellulose, which appears white, remains after lignin decay (Fukasawa, 2021). By contrast, brown rot wood appears darker as lignin remains after cellulose decay (Fukasawa, 2021). Both beech and fir can be characterized by white and brown rot fungi and the prevalence of fungal species with specific decay characteristics depend on numbers of factors

(e.g., environmental conditions but also stochastic processes) (Boddy, 2001; Brabcová et al., 2022). To illuminate this potential explanation, one would need data on the prevailing type of decay caused by specific fungi and the related color lightness. Another explanation could be differences in moisture conditions between fir and beech deadwood. It has been shown that in general a higher moisture content tends to buffer temperature extremes (Davis et al., 2019). Furthermore, differences in wood physical characteristics caused by specific decay processes can be related to differences in the water-holding capacity of the deadwood object (Přívětivý and Šamonil, 2021). Thus, a higher level of wood moisture in fir than in beech might cause lower temperatures in the growing season. In addition, bryophyte cover, which was from our observation higher on fir than on beech logs, can buffer microclimatic extremes. In several studies it has been suggested that bryophyte cover stores water, thereby cooling the deadwood object (Heilmann-Clausen and Christensen, 2005; Pouska et al., 2017). However, our study lacks the relevant data to fully elucidate these underlying mechanisms. Therefore, further research is needed to explore the effects of deadwood physical properties, including surface structure and color changes, on internal temperature as decay progresses.

5. Conclusion

Our study revealed that temperature inside deadwood is primarily influenced by canopy openness. The other stand-scale factor (amount of deadwood) and object-scale factors (diameter, tree species, position) had only weak effects. We conclude that the large-scale disturbances by land use and climate change strongly affect deadwood temperature. This might have severe consequences on ecosystem functions and services provided by deadwood, such as habitat conditions, ecosystem resilience, as well as water-, carbon- and nutrient cycling. However, further studies are needed to quantify these relationships at various spatial scales.

CRediT authorship contribution statement

Jasper Schreiber: Writing – original draft, Methodology, Formal analysis. **Václav Pouska:** Writing – review & editing, Data curation, Conceptualization. **Petr Macek:** Writing – review & editing, Data curation, Conceptualization. **Dominik Thom:** Writing – review & editing. **Claus Bässler:** Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2024.110378.

Data availability

Data will be made available on request.

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"Effects of canopy-mediated microclimate and object characteristics on deadwood temperature"

Supplementary Information

Tab. S1 List of the 50 deadwood objects in which temperature was measured from May 2016 to October 2019 with the corresponding object and environmental characteristics.

Object	Block	Plot	Canopy cover	Surrounding deadwood [m^3/ha]	Tree species	Position	Diameter [m]
AG18-081-B-C	A	AG18	closed	24.68	beech	uplifted	0.31
AG18-082-B-C	A	AG18	closed	24.68	beech	lying	0.32
AG18-083-T-C	A	AG18	closed	24.68	fir	lying	0.28
AG18-084-T-C	A	AG18	closed	24.68	fir	lying	0.25
AG19-089-B-C	A	AG19	closed	161.46	beech	lying	0.33
AG19-090-B-C	A	AG19	closed	161.46	beech	uplifted	0.42
AG19-091-T-C	A	AG19	closed	161.46	fir	lying	0.29
AG19-092-T-C	A	AG19	closed	161.46	fir	uplifted	0.29
AO09-137-B-C	A	AO09	open	145.64	beech	lying	0.39
AO09-138-B-C	A	AO09	open	145.64	beech	lying	0.38
AO09-139-T-C	A	AO09	open	145.64	fir	lying	0.24
AO09-140-T-C	A	AO09	open	145.64	fir	lying	0.38
AO09-T-C-1	A	AO09	open	145.64	fir	uplifted	0.22
AO09-T-C-2	A	AO09	open	145.64	fir	lying	0.21
AO09-T-C-3	A	AO09	open	145.64	fir	uplifted	-
BG11-241-B-C	B	BG11	closed	168.75	beech	lying	0.19
BG11-242-B-C	B	BG11	closed	168.75	beech	uplifted	0.24
BG11-243-T-C	B	BG11	closed	168.75	fir	lying	0.45
BG11-244-T-C	B	BG11	closed	168.75	fir	uplifted	0.31
BO09-329-B-C	B	BO09	open	165.20	beech	lying	0.27
BO09-330-B-C	B	BO09	open	165.20	beech	uplifted	0.28
BO09-331-T-C	B	BO09	open	165.20	fir	lying	0.29
BO09-332-T-C	B	BO09	open	165.20	fir	uplifted	0.31
BO14-354-B-C	B	BO14	open	24.77	beech	uplifted	0.30
BO14-355-B-C	B	BO14	open	24.77	beech	lying	0.33
BO14-356-B-C	B	BO14	open	24.77	beech	lying	0.33
DG07-602-B-C	D	DG07	closed	26.34	beech	lying	0.48
DG07-603-T-C	D	DG07	closed	26.34	fir	lying	0.31
DG07-604-T-C	D	DG07	closed	26.34	fir	uplifted	0.44
DG14-641-B-C	D	DG14	closed	190.00	beech	uplifted	0.29
DG14-642-B-C	D	DG14	closed	190.00	beech	lying	0.38
DG14-643-T-C	D	DG14	closed	190.00	fir	lying	0.46
DG14-644-T-C	D	DG14	closed	190.00	fir	uplifted	0.29
DG14-B-C	D	DG14	closed	190.00	beech	uplifted	0.26
DO01-673-T-C	D	DO01	open	157.48	fir	uplifted	0.34

DO01-675-T-C	D	DO01	open	157.48	fir	lying	0.37
DO01-676-T-C	D	DO01	open	157.48	fir	lying	0.35
DO10-717-B-C	D	DO10	open	185.54	beech	uplifted	0.31
DO10-718-B-C	D	DO10	open	185.54	beech	lying	0.40
DO10-719-T-C	D	DO10	open	185.54	fir	uplifted	0.21
DO10-B-C	D	DO10	open	185.54	beech	uplifted	0.31
EG02-773-B-C	E	EG02	closed	221.15	beech	uplifted	0.37
EG02-774-B-C	E	EG02	closed	221.15	beech	lying	0.38
EG02-775-T-C	E	EG02	closed	221.15	fir	lying	0.41
EG02-776-T-C	E	EG02	closed	221.15	fir	uplifted	0.39
EO17-941-B-C	E	EO17	open	214.91	beech	lying	0.37
EO17-942-B-C	E	EO17	open	214.91	beech	uplifted	0.35
EO17-943-T-C	E	EO17	open	214.91	fir	lying	0.31
EO17-944-T-C	E	EO17	open	214.91	fir	uplifted	0.34
EO17-B-C	E	EO17	open	214.91	beech	uplifted	0.42

Tab. S2 Number of objects in closed and open canopies for each year and month. Note missing data for January due to snow cover, see Method section.

Month	2016		2017		2018		2019	
	closed	open	closed	open	closed	open	closed	open
02			17	15	12	1	8	0
03			20	19	14	5	20	4
04			20	20	19	12	22	18
05	24	26	20	20	19	11	22	7
06	24	26	22	25	19	11	23	7
07	24	23	22	25	24	17	23	7
08	24	19	21	18	24	14	24	7
09	23	19	21	15	24	15	24	7
10	23	19	20	15	23	15	23	7
11	23	24	19	12	23	13		
12	11	6	6	0	23	12		

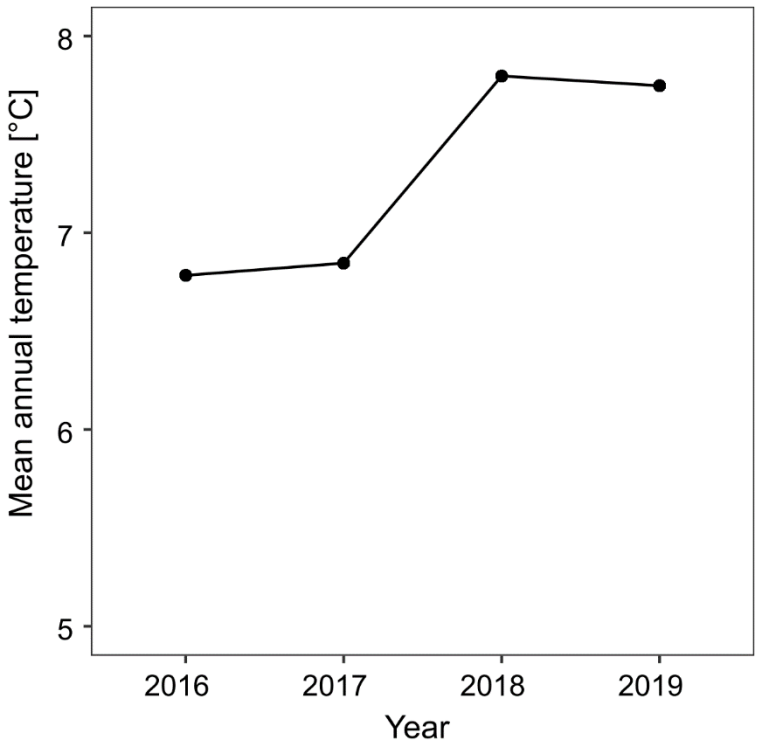

Figure S1 Mean annual temperature for each year retrieved from the meteorological station Waldhäuser (between 1 km and 11 km away from our sites), which were used as covariate and as an offset argument to account for the annual difference in mean temperature in the linear-mixed effect models.

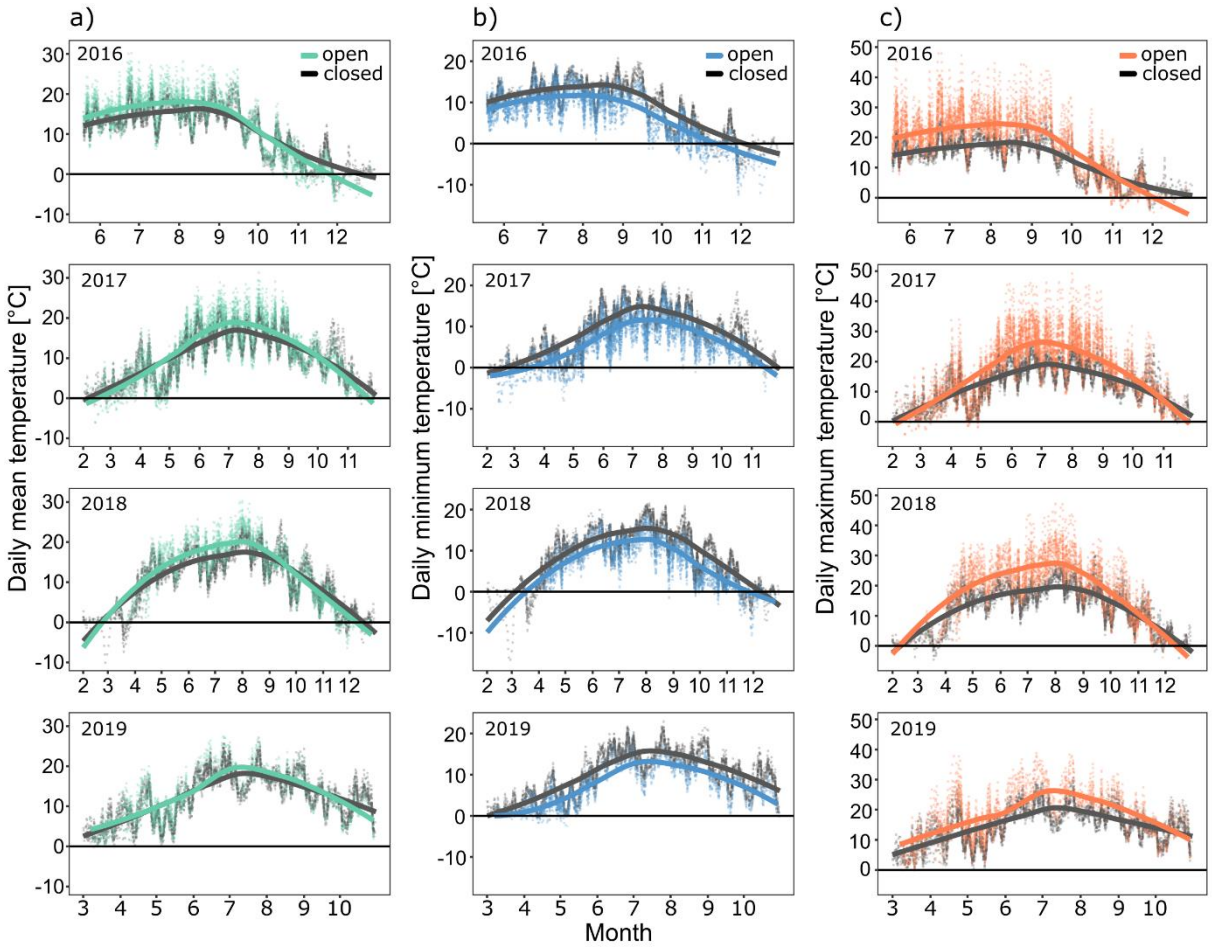

Figure S2 Daily a) mean, b) minimum and c) maximum temperature values in open and closed canopies of each deadwood object (dotted lines) and 'loess' curves (solid lines, to detect all possible trends) of the respective mean values from 2016-2019. Note that the x-axes (month) differ among years due to the removal of data caused by snow cover or logger failures.

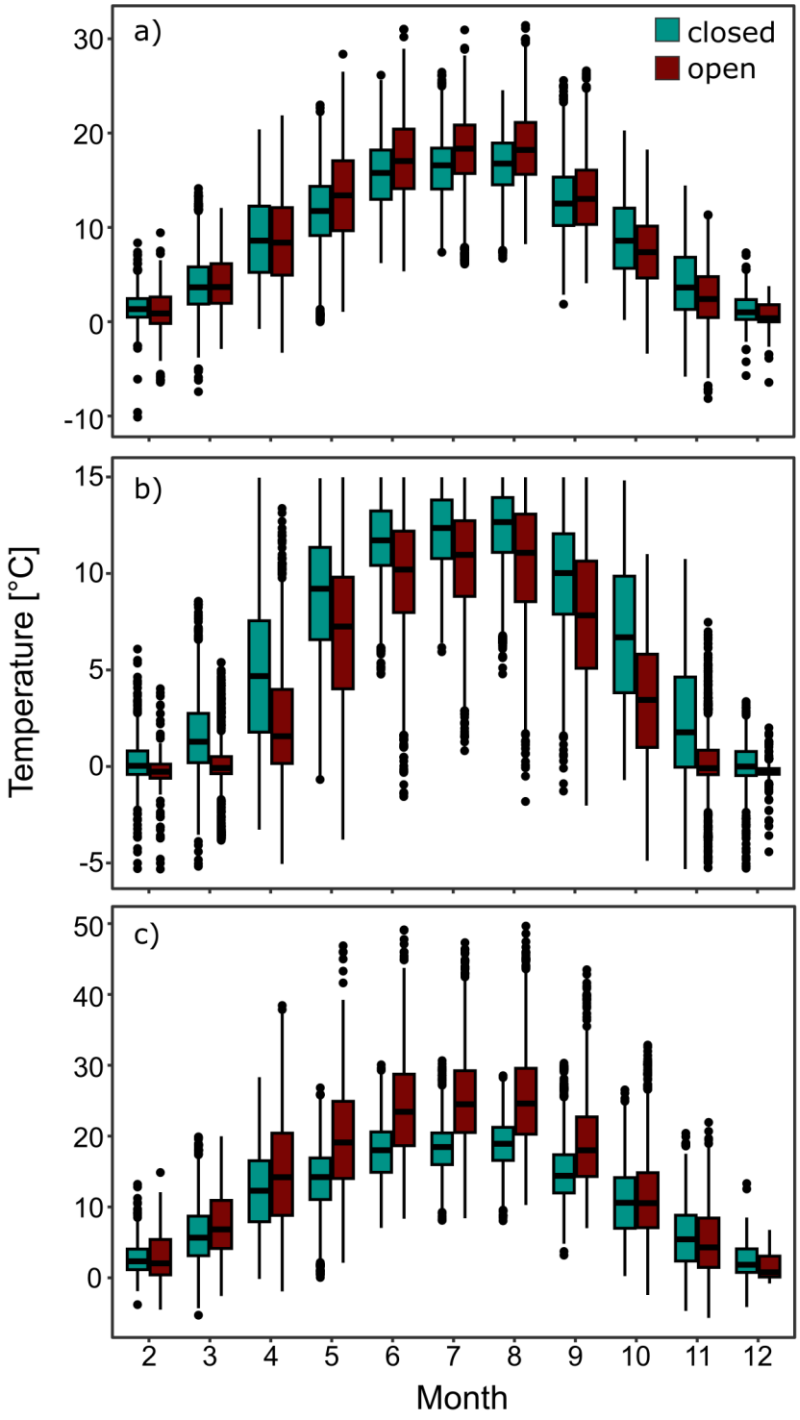

Figure S3 Observed data of daily a) mean, b) minimum and c) maximum temperature within deadwood in open versus closed canopies in each month across years (2016-2019).

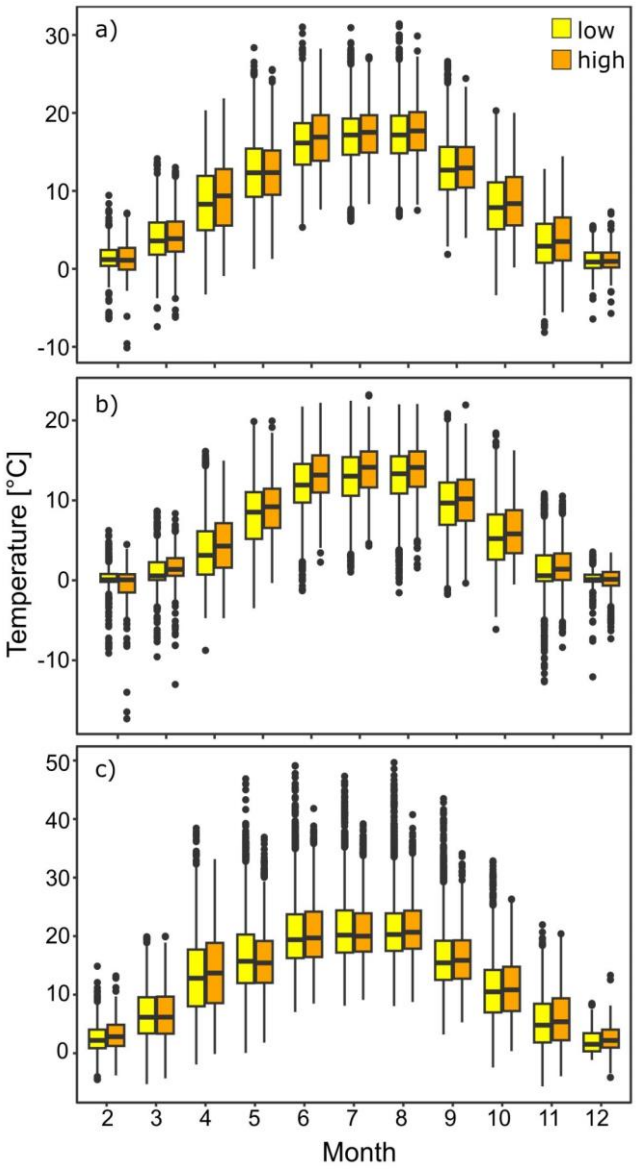

Figure S4 Observed data of daily a) mean, b) minimum and c) maximum temperature within deadwood in low versus high amount of surrounding deadwood on a plot in each month across years (2016-2019). We used the two categories low and high amount of dead wood to increase visibility and to provide consistent plots across our predictor set. Low amount of dead wood is defined as an average of 25.20 m^3/ha and high amount of dead wood is defined as an average of 178.12 m^3/ha.

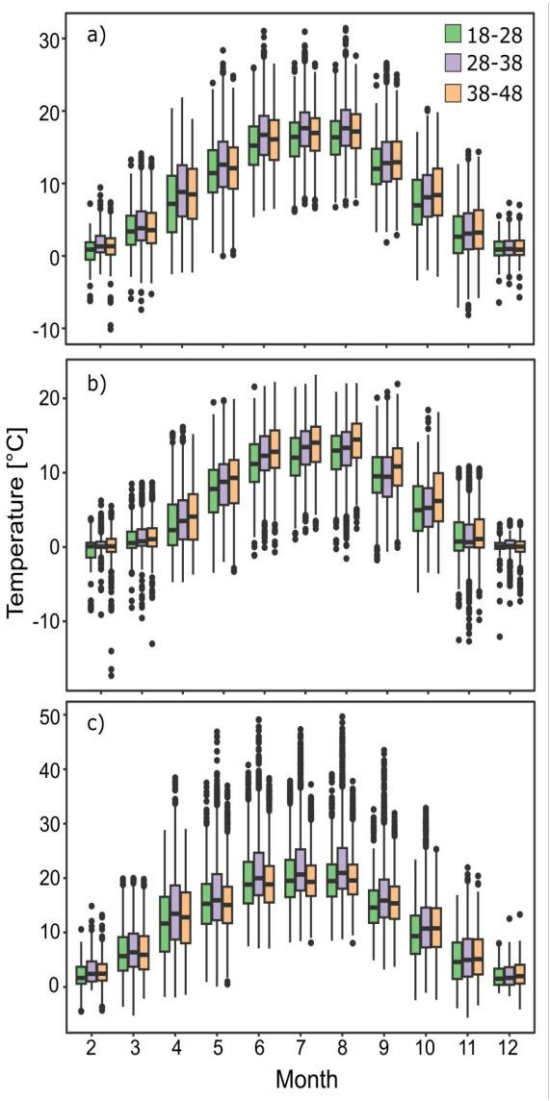

Figure S5 Observed data of daily a) mean, b) minimum and c) maximum temperature within deadwood in different diameter categories (18-28 cm, 29-38 cm, 39-48 cm) in each month across years (2016-2019). Diameter categories were used for the plots to increase visibility and to provide consistent plots across our predictor set. Categories were chosen based on histograms of the raw distribution of diameter values across our data set. The first category (18-28 cm) included eleven objects, the second category (29-38 cm) included 28 objects, and the third category (39-48 cm) included ten objects.

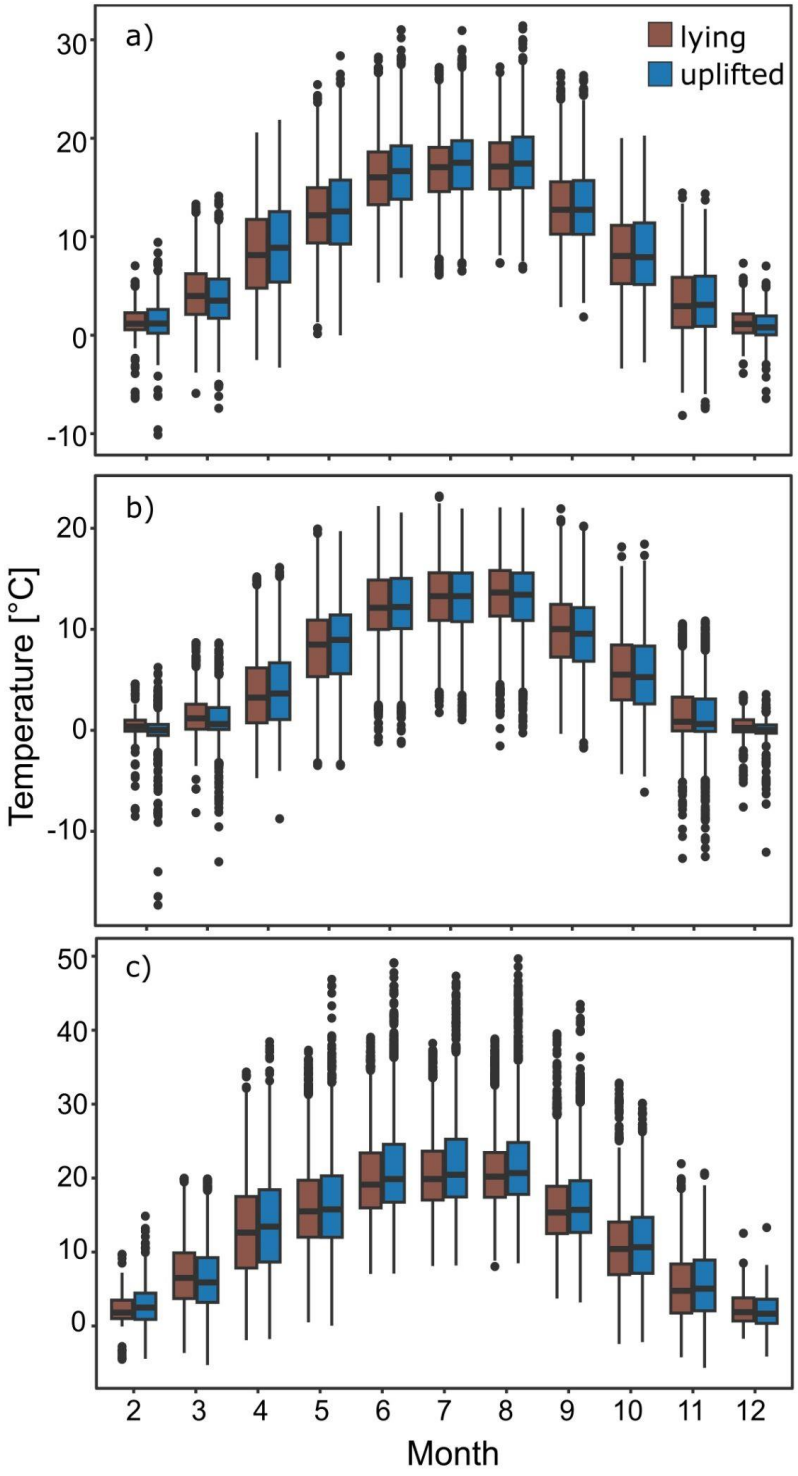

Figure S6 Observed data of daily a) mean, b) minimum and c) maximum temperature within deadwood in lying versus uplifted deadwood objects in each month across years (2016-2019).

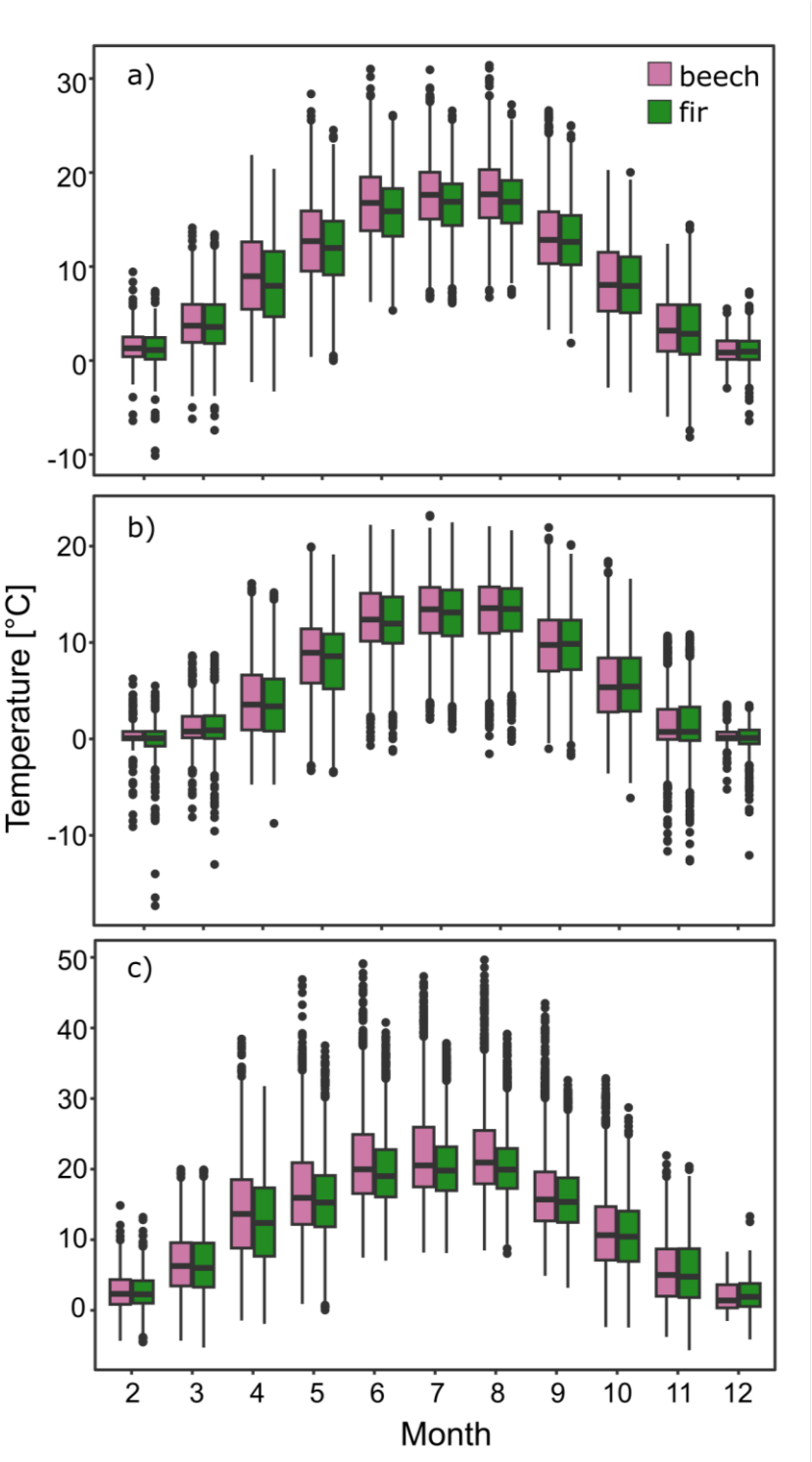

Figure S7 Observed data of daily a) mean, b) minimum and c) maximum temperature within deadwood in beech versus fir deadwood objects in each month across years (2016-2019).

Table S3 Results (t-values=predictor estimate divided by SD) of the monthly models (based on aggregated daily values, see method section) testing stand and object scale variables on deadwood mean, minimum and maximum temperature across the years 2016-2019 with annual temperatures as offset. A positive t-value indicates higher temperature values in the reference group (open canopy, uplifted position, fir deadwood) or an increase in temperature with increasing deadwood amount and object diameter (see method section). Conversely, a negative t-value indicates lower temperature values in the reference group or a decrease in temperature with increasing deadwood amount and object diameter. Values in bold represent significant t-values. Significance levels are *: p-value < 0.05, **: p-value < 0.01, ***: p-value < 0.001. The marginal R^2 represents the explained variance by the fixed effects (stand and object scale variables) in each model. Note that January is not shown due unreliable data caused by high numbers of days with snow cover.

Month	Canopy (reference = "open")			Deadwood amount			Object diameter			Position (reference = "uplifted")			Tree species (reference = fir)			Marginal R^2		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max
2	-1.35	-2.06	-0.44	1.44	2.21	0.42	-0.54	-0.75	-0.16	-0.41	-1.38	0.56	-0.5	-1.24	0.19	*0.15*	*0.29*	*0.03*
3	1.01	-2.24	**3.13***	-1.52	-0.37	-1.77	-1.2	-0.99	-1.18	**-2.11***	-1.64	**-2.17***	-0.13	-0.58	0.18	*0.13*	*0.14*	*0.23*
4	-0.24	**-3.59***	1.37	-0.92	-0.48	-0.78	0.13	0.86	-0.17	0.56	0.72	0.4	-0.51	-0.74	-0.3	*0.03*	*0.32*	*0.07*
5	**4.87****	-2.27	**5.18****	-0.49	-0.02	0.11	-0.09	0.45	-0.42	0.39	0.36	0.08	-1.34	-0.69	-1.28	*0.19*	*0.05*	*0.43*
6	**2.78***	**-3.78****	**4.43****	-1.11	-0.35	-0.22	0.08	1.11	-0.3	0.83	0.14	0.88	-1.29	-0.86	-1.02	*0.18*	*0.42*	*0.46*
7	**2.84***	**-3.90****	**4.11****	-0.52	-0.24	0.05	0.69	1.69	-0.09	0.35	0.43	0.09	**-2.75****	-1.42	-1.95	*0.30*	*0.46*	*0.54*
8	**3.99***	**-4.37****	**4.31****	-1.74	-0.46	-0.08	-0.14	1.31	-0.71	0.58	0.01	0.6	**-2.44***	-1.92	-1.24	*0.30*	*0.53*	*0.54*
9	**2.35***	**-5.53*****	**3.46***	-1.38	0.02	-0.04	-0.01	0.77	-0.68	0.27	-0.45	0.36	-1.5	-0.85	-0.85	*0.06*	*0.37*	*0.32*
10	**-2.59***	**-4.84****	1.78	-1.68	0.03	**-2.65***	-0.36	0.45	-0.68	0.19	-0.68	0.82	-0.85	-1.25	-0.64	*0.12*	*0.50*	*0.08*
11	**-3.42***	**-4.14****	-2.13	-0.74	-0.09	-1.53	-0.28	0.51	-0.66	-0.04	-1.44	0.83	-0.9	-1.06	-0.64	*0.29*	*0.45*	*0.13*
12	**-4.02****	**-2.68***	**-3.31***	-0.36	0.78	-1.38	**-2.14***	-1.27	-1.08	-0.94	-1.31	-0.11	-0.29	-1.27	0.99	*0.47*	*0.23*	*0.34*

Table S4 Results (t-values=predictor estimate divided by SD) of the seasonal models testing stand and object scale variables on deadwood mean, minimum and maximum temperature. Models are based on the years 2016-2019. Seasons were meteorologically defined for our study area (see method section). The values in brackets indicate the months considered in the seasons. A positive t-value indicates higher temperature values in the reference group (open canopy, uplifted position, fir deadwood) or an increase in temperature with increasing deadwood amount and object diameter (see method section). Conversely, a negative t-value indicates lower temperature values in the reference group or a decrease in temperature with increasing deadwood amount and object diameter. Values in bold represent significant t-values. Significance levels are (*: p-value < 0.05, **: p-value < 0.01, ***: p-value < 0.001). The marginal R^2 represents the explained variance by the fixed effects (stand and object scale variables) in each model. Note that January is not shown due unreliable data caused by high numbers of days with snow cover.

Season	Canopy (reference "open")			Deadwood amount			Object diameter			Position (reference "uplifted")			Tree species (reference "fir")			Marginal R^2		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Spring (3-5)	-0.21	-1.84	**2.66***	-0.52	-0.52	-0.92	0.56	0.56	1	0.59	0.5	1.03	-0.68	-0.66	-1.36	*0.40*	*0.41*	*0.34*
Summer (6-8)	**11.48*****	**-4.21****	**4.09****	**-6.34*****	-0.34	-0.06	-0.32	1.79	-1.15	**2.56***	0.08	1.26	**-5.24*****	**-2.17***	**-2.83****	*0.10*	*0.19*	*0.27*
Autumn (9-11)	-0.21	**-7.2*****	**4.75****	-0.07	-0.01	-0.15	1.28	0.99	1.89	0.57	-0.43	1.38	-0.67	-0.55	-0.97	*0.24*	*0.24*	*0.17*
Winter (12-2)	-1.67	-1.75	-1.45	0.36	0.73	-0.22	-1.28	-0.92	-1.22	-0.86	-1.87	0.43	-1.28	-1.96	-0.28	*0.06*	*0.08*	*0.03*

Table S5 Full model results of the monthly and seasonal models testing stand and object scale variables on deadwood mean, minimum and maximum temperature. Models are based on the years 2016-2019. Growing season (May-October) versus winter (November-April, without January) were defined based on biological data of the study area (see method section). A positive t-value indicates higher temperature values in the reference group (open canopy, uplifted position, fir deadwood) or an increase in temperature with increasing deadwood amount and object diameter (see method section). Conversely, a negative t-value indicates lower temperature values in the reference group or a decrease in temperature with increasing deadwood amount and object diameter. Values in bold represent significant t-values. Note that January is not shown due to unreliable data caused by high numbers of days with snow cover. Est. = Estimate, SD= Standard deviation, t= t-value, p= p-value.

			Canopy (reference "open")				Deadwood amount				Object diameter				Position (reference "uplifted")				Tree species (reference "fir")			
			Est.	SD	t	p	Est.	SD	t	p	Est.	SD	t	p	Est.	SD	t	p	Est.	SD	t	p
Month	2	Mean	-1.02	0.53	-1.95	0.099	0.51	0.48	1.06	0.328	-0.2	0.26	-0.77	0.444	-0.09	0.23	-0.39	0.695	-0.17	0.21	-0.79	0.429
		Min	**-1.28**	**0.51**	**-2.49**	**0.047**	0.88	0.46	1.9	0.105	-0.25	0.33	-0.74	0.461	-0.43	0.31	-1.37	0.173	-0.35	0.29	-1.2	0.233
		Max	-0.69	0.55	-1.25	0.257	-0.11	0.54	-0.21	0.844	-0.18	0.25	-0.74	0.459	0.29	0.22	1.32	0.187	-0.02	0.2	-0.09	0.928
	3	Mean	-0.76	0.56	-1.34	0.228	-0.47	0.58	-0.82	0.445	0.52	0.58	0.9	0.367	0.49	0.57	0.86	0.388	-0.3	0.53	-0.56	0.573
		Min	**-1.01**	**0.26**	**-3.88**	**0.008**	-0.14	0.26	-0.54	0.607	-0.04	0.14	-0.25	0.803	-0.03	0.13	-0.24	0.811	-0.17	0.12	-1.42	0.157
		Max	-0.69	0.55	-1.25	0.257	-0.89	0.69	-1.29	0.245	0.51	0.68	0.75	0.454	0.58	0.66	0.88	0.382	-0.28	0.62	-0.44	0.657
	4	Mean	-0.01	0.3	-0.03	0.975	-0.04	0.29	-0.14	0.894	0.42	0.32	1.31	0.19	0.43	0.31	1.39	0.166	-0.29	0.3	-0.98	0.326
		Min	**-1.38**	**0.17**	**-8.36**	**0**	-0.22	0.17	-1.3	0.243	0.13	0.18	0.71	0.479	0.14	0.16	0.88	0.377	-0.14	0.15	-0.91	0.362
		Max	1	0.74	1.35	0.224	-0.67	0.73	-0.92	0.393	-0.14	0.48	-0.3	0.767	0.21	0.41	0.5	0.614	-0.2	0.41	-0.48	0.63
	5	Mean	0.42	0.42	1.01	0.35	-0.31	0.4	-0.77	0.473	0.16	0.29	0.55	0.583	0.22	0.25	0.89	0.376	-0.31	0.25	-1.24	0.214
		Min	**-1.34**	**0.47**	**-2.87**	**0.028**	-0.16	0.43	-0.37	0.724	0.25	0.25	0.98	0.328	0.19	0.22	0.88	0.379	-0.21	0.22	-0.94	0.35
		Max	**2.35**	**0.57**	**4.12**	**0.006**	-0.15	0.54	-0.27	0.796	-0.05	0.26	-0.17	0.862	0.14	0.22	0.64	0.521	-0.32	0.22	-1.44	0.151
	6	Mean	**1**	**0.14**	**6.98**	**0**	**-0.54**	**0.15**	**-3.68**	**0.01**	0.02	0.15	0.1	0.919	0.25	0.14	1.8	0.072	**-0.36**	**0.13**	**-2.66**	**0.008**
		Min	**-1.25**	**0.32**	**-3.94**	**0.008**	-0.12	0.29	-0.4	0.706	0.17	0.12	1.41	0.159	0.04	0.1	0.36	0.718	-0.08	0.1	-0.8	0.422
		Max	**3.24**	**0.74**	**4.39**	**0.005**	-0.15	0.69	-0.21	0.837	-0.08	0.18	-0.44	0.661	0.21	0.16	1.31	0.191	-0.23	0.16	-1.42	0.156
	7	Mean	**0.78**	**0.19**	**4.12**	**0.006**	**-0.53**	**0.2**	**-2.68**	**0.037**	-0.04	0.2	-0.18	0.854	0.24	0.19	1.27	0.205	**-0.44**	**0.18**	**-2.45**	**0.014**
		Min	**-1.52**	**0.42**	**-3.57**	**0.012**	-0.11	0.4	-0.28	0.791	0.14	0.16	0.89	0.373	0.01	0.14	0.09	0.929	-0.17	0.14	-1.17	0.243
		Max	**3.36**	**0.79**	**4.24**	**0.005**	-0.02	0.75	-0.03	0.976	-0.1	0.17	-0.55	0.584	0.08	0.15	0.52	0.601	-0.28	0.15	-1.81	0.071
	8	Mean	**0.85**	**0.32**	**2.66**	**0.038**	-0.31	0.32	-0.99	0.362	0	0.13	0.02	0.987	0.06	0.11	0.58	0.561	**-0.25**	**0.11**	**-2.17**	**0.03**
		Min	**-1.44**	**0.28**	**-5.12**	**0.002**	-0.1	0.26	-0.39	0.711	0.16	0.11	1.36	0.174	-0.01	0.1	-0.09	0.925	-0.16	0.1	-1.65	0.099
		Max	**3.07**	**0.82**	**3.72**	**0.01**	0	0.77	0	0.998	-0.13	0.15	-0.87	0.385	0.1	0.12	0.79	0.43	**-0.26**	**0.13**	**-2.03**	**0.042**
	9	Mean	0.15	0.28	0.52	0.624	-0.02	0.25	-0.09	0.931	0.18	0.22	0.81	0.416	0.01	0.19	0.05	0.962	-0.18	0.19	-0.92	0.358
		Min	**-1.61**	**0.16**	**-9.93**	**0**	-0.05	0.14	-0.35	0.74	0.23	0.16	1.4	0.162	-0.1	0.16	-0.6	0.549	-0.08	0.16	-0.52	0.605

		Max	**1.98**	**0.25**	**8.02**	**0**	-0.52	0.23	-2.22	0.077	-0.09	0.25	-0.34	0.731	0.12	0.22	0.56	0.573	-0.37	0.21	-1.73	0.083
		Mean	**-0.5**	**0.2**	**-2.51**	**0.046**	0.03	0.18	0.15	0.884	**0.43**	**0.2**	**2.14**	**0.032**	0.18	0.2	0.92	0.358	-0.19	0.19	-1.01	0.315
	10	Min	**-1.76**	**0.41**	**-4.33**	**0.005**	-0.01	0.38	-0.04	0.97	0.06	0.16	0.36	0.719	-0.06	0.13	-0.47	0.638	-0.14	0.14	-1.06	0.291
		Max	0.18	0.45	0.4	0.7	-0.57	0.46	-1.25	0.259	-0.2	0.25	-0.81	0.418	0.13	0.21	0.64	0.523	-0.2	0.21	-0.94	0.346
		Mean	-0.51	0.35	-1.49	0.187	-0.13	0.32	-0.42	0.687	0.11	0.35	0.32	0.752	0.09	0.35	0.26	0.796	-0.03	0.34	-0.09	0.93
	11	Min	**-1.1**	**0.22**	**-5.07**	**0.002**	-0.04	0.2	-0.18	0.864	0.06	0.22	0.26	0.797	-0.13	0.22	-0.59	0.556	-0.07	0.21	-0.35	0.729
		Max	0	0.31	0	0.998	-0.19	0.28	-0.68	0.523	0.17	0.31	0.55	0.581	0.29	0.31	0.95	0.34	-0.02	0.3	-0.08	0.937
		Mean	**-0.36**	**0.11**	**-3.24**	**0.023**	0	0.08	-0.04	0.969	-0.06	0.09	-0.62	0.533	-0.11	0.1	-1.1	0.271	-0.01	0.09	-0.09	0.931
	12	Min	-0.3	0.13	-2.33	0.067	0.12	0.1	1.16	0.298	-0.1	0.1	-1	0.318	-0.16	0.1	-1.59	0.113	-0.14	0.1	-1.45	0.147
		Max	**-0.41**	**0.15**	**-2.67**	**0.044**	-0.15	0.12	-1.3	0.249	-0.01	0.13	-0.1	0.918	-0.04	0.14	-0.29	0.773	0.12	0.13	0.93	0.353
Season	Growing	Mean	**0.96**	**0.15**	**6.57**	**0.001**	-0.28	0.15	-1.92	0.103	-0.05	0.15	-0.34	0.737	0.1	0.14	0.71	0.475	**-0.31**	**0.13**	**-2.29**	**0.022**
		Min	**-1.12**	**0.11**	**-9.87**	**0**	-0.09	0.11	-0.79	0.461	0.16	0.12	1.37	0.172	-0.03	0.11	-0.31	0.76	-0.12	0.11	-1.13	0.259
		Max	**2.81**	**0.14**	**20.47**	**0**	**-0.53**	**0.14**	**-3.83**	**0.009**	-0.25	0.15	-1.74	0.083	0.25	0.13	1.95	0.052	**-0.51**	**0.13**	**-4.09**	**0**
	Winter	Mean	0.06	0.2	0.3	0.776	-0.15	0.19	-0.75	0.482	-0.04	0.21	-0.17	0.862	-0.1	0.19	-0.55	0.584	-0.22	0.18	-1.18	0.236
		Min	**-0.91**	**0.12**	**-7.73**	**0**	0.08	0.11	0.73	0.495	0.01	0.12	0.11	0.911	-0.15	0.11	-1.35	0.178	-0.19	0.11	-1.78	0.074
		Max	**1**	**0.34**	**2.91**	**0.027**	-0.31	0.34	-0.91	0.398	-0.1	0.29	-0.33	0.74	-0.13	0.26	-0.5	0.62	-0.16	0.25	-0.65	0.517

10.2 Effects of experimental canopy openness on wood-inhabiting fungal fruiting diversity across succession

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Effects of experimental canopy openness on wood-inhabiting fungal fruiting diversity across succession

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While the succession of terrestrial plant communities is well studied, less is known about succession on dead wood, especially how it is affected by environmental factors. While temperate forests face increasing canopy mortality, which causes considerable changes in microclimates, it remains unclear how canopy openness affects fungal succession. Here, we used a large real-world experiment to study the effect of closed and opened canopy on treatment-based alpha and beta fungal fruiting diversity. We found increasing diversity in early and decreasing diversity at later stages of succession under both canopies, with a stronger decrease under open canopies. However, the slopes of the diversity versus time relationships did not differ significantly between canopy treatments. The community dissimilarity remained mainly stable between canopies at ca. 25% of species exclusively associated with either canopy treatment. Species exclusive in either canopy treatment showed very low number of occupied objects compared to species occurring in both treatments. Our study showed that canopy loss subtly affected fungal fruiting succession on dead wood, suggesting that most species in the local species pool are specialized or can tolerate variable conditions. Our study indicates that the fruiting of the fungal community on dead wood is resilient against the predicted increase in canopy loss in temperate forests.

Keywords Succession, Microclimate, Canopy mortality, Climate change, Fungi, Dead wood, Forest management

Forests are increasingly subjected to canopy mortality due to disturbances, forest management and climate change[1–3]. Especially disturbances and droughts increase canopy mortality, and the death of trees leads to the aggregation of dead wood if not removed due to pest control[4]. Open canopies lead to increased sun exposure and higher variability of temperature and moisture and thus create a variable environment, whereas microclimates below closed canopies buffer sun exposure and create more constant thermal and moisture conditions[5–7]. Further, forest canopies likely exceed 30 years to recover to pre-disturbance conditions such as canopy closure, which can even take longer if repeated disturbances cause recurring canopy loss[2,8,9]. Since dead wood decays over years to decades[10], depending on the size, organisms may face increasingly open canopies and associated changes in microclimate throughout the successional stages of wood-inhabiting organisms. Although several studies have shown that open canopy conditions affect various species groups' richness and community composition on dead

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wood[11–15], we have only a limited understanding of the succession of wood-inhabiting organisms in general and under contrasting canopy conditions, hampering predictions under future conditions such as increasing canopy loss[16].

Fruit body-forming fungi are among the most diverse colonizers of dead wood, besides insects such as bark beetles[17–19]. Several studies have shown significant effects of canopy cover or canopy openness on wood-inhabiting fungal diversity[13,14,20,21]. For example, a real-world experiment found that the richness of wood-inhabiting fungi was non-significantly higher under closed compared with open canopies. Further, the composition differed significantly between closed and open canopies for two tree species[13]. Such previous studies mainly investigated the first years and stages of decay[13,22], did not explicitly analyze succession[23], focused on a subset of the fungal taxonomic breadth[24], or surveyed different decay stages simultaneously of different dead wood items instead of following succession on the same items[25–29]. Therefore, we know little about the succession of fungal species on standardized dead wood objects in different microclimates. Studies investigating succession found a peak of species diversity at intermediate decay stages for fruit body data[30] and at final decay stages for metabarcoding data[30,31]. Further, the succession was affected by the species composition of the initial colonizers causing priority effects[32]. Since wood-inhabiting fungi undergo a succession of species during decay[29], one might expect differences in successional patterns with time between forest microclimate conditions[33,34]. Since moisture and temperature are important factors affecting fungal growth, canopy openness can be expected to affect species richness and community composition across successional stages[13,14,35–40]. For example, wood-inhabiting species were shown to be differentially tolerant to temperature and moisture[15,41]. If species that colonize at different time points are differentially tolerant to microclimates, we would expect differences in the successional pattern of richness and composition. Based on these prior results, we hypothesize (i) increasing difference in alpha diversity due to lowering species numbers under open canopies if fewer species can tolerate variable microclimatic conditions (ii) increasing difference in community dissimilarity from early and late stages of decay because of species reduction under open canopies.

To address these hypotheses, we established a dead wood experiment with 240 dead wood logs and 480 dead wood branches of two host tree species (*Fagus sylvatica*, hereafter "beech", and *Abies alba*, hereafter "fir") half of them were exposed to closed canopies, while the other half to open canopies (Fig. 1A,B). Visible fungal species of Asco- and Basidiomycota were identified on each dead wood log and branch for 10 consecutive years (Fig. 1C). Canopies were kept open, and ground vegetation was mowed yearly to disentangle the effects of canopy-mediated microclimatic conditions from other edaphic factors affecting fungal performance during succession. We calculated treatment-based alpha and beta diversity (Fig. 1D) and compared them across the successional years (Fig. 1E). We further weighted the importance of species by their incidence frequency (number of dead wood objects occupied) to emphasize rare, common and dominant species along the Hill series (Fig. 1F)[42].

Material and methods

Study area and study design

The dead-wood experiment was established in the management zone of the Bavarian Forest National Park in southeastern Germany in 2011 (Fig. 1A). The management zone is characterized by a mixed mountain forest with Norway spruces (*Picea abies* (L.) H. Karst), European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.)[43]. Mean annual temperature in this zone is ca. 7 °C and mean sum of annual precipitation ca. 1300 mm[44].

We created 36 plots with a size of 0.1 ha, which we replicated in 5 blocks across the landscape scale (Fig. 1A). Half of the plots were created under closed canopies (18) and half under open canopies (18) (Fig. 1B). The open canopies resulted from removing all living and dead trees from the plots. Annual mowing kept the plots open. Within the 18 plots, different combinations of dead wood tree species and dead wood types were designed to capture differences in dead-wood heterogeneity on the plot level. The combinations are shown within a schematic (Fig. 1B) and are described in detail in Refs. [12,13]. In summary, across all five blocks and both canopy treatments, a total of 240 logs (5 blocks * 2 tree species * 24 logs) and 480 branches (5 blocks * 2 tree species * 48 branches) were placed on the forest floor. Seven dead wood objects could not be used for analysis because the objects themselves (branches) or their labels could not be found (stolen or broken off). The logs had a mean diameter of +/− SD = 33 +/− 6.5 cm, and a standardized length of 5 m. The branches had a mean diameter of +/− SD = 3.2 +/− 1.3 cm, and a mean length +/− SD = 2.7 +/− 0.88 m. The logs and branches were from stands of similar elevation, tree species composition, age, and size and were harvested with chainsaws and brought to the plots at the end of 2011.

Previous studies showed considerable and significant dead wood object surface temperature differences of ca. 20 °C on average for a summer day between open and closed canopies within the same experiment[21,45]. We measured wood surface temperatures on the upper surface of 136 logs, with each of five measures for every meter (segment) of the log (half under open, half under closed plots across the four blocks) in August 2018 using an infrared thermal sensor on a summer day. We found great differences in Light Detection and Ranging (LiDAR) penetration rate and temperature between open and closed canopies (Fig. S1). The LiDAR penetration rate is a reliable measure of radiation availability near the ground[46].

Fruit body inventories

We identified species based on fruit bodies that were visible with the naked eye on dead wood objects every autumn (September/October), the main season of fruit body development (Fig. 1C)[47]. To ensure an effective and non-redundant sampling, we divided logs into seven segments, each 1 m long. Two segments represented the log's cut edges, and five represented the log surface. The branches were considered as a single segment. Fruit bodies were identified in the field or, if necessary, in the laboratory with the aid of a microscope by mycological professionals (see *Acknowledgements*). Voucher specimens were deposited in the herbarium of the Bavarian Forest

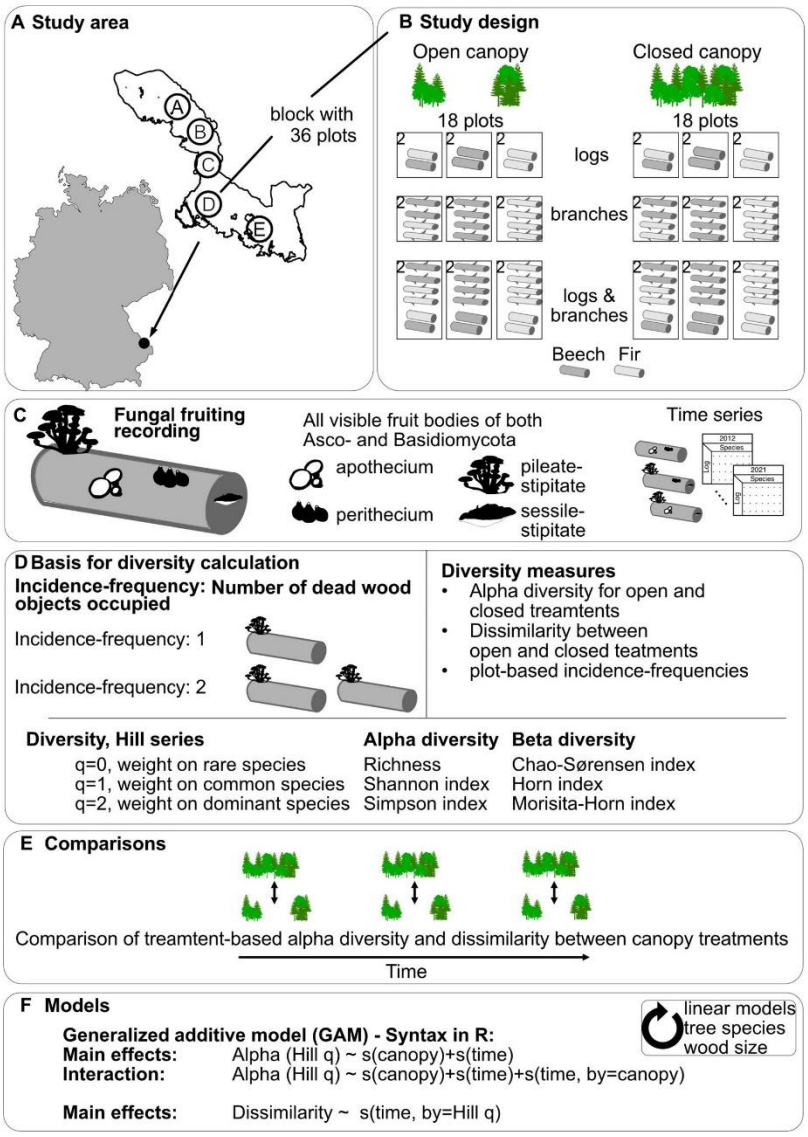

Figure 1. Conceptual graphic of the study design and analysis workflow. (**A**) The location of the National Park Bavarian Forest in the southeast of Germany with the alphabetical denotation showing the 5 random blocks of the dead wood experiment. (**B**) Within each block 18 plots are closed canopy stands and 18 result from 0.1 ha clearings of woody plants and yearly mowing. Within each plot, logs and/or branches of Beech and/or Fir were installed. (**C**) All visible fungal specimens were identified based on reproductive structures (fruit bodies) on all dead wood objects across a time series of 10 consecutive years. (**D**) Based on the dead wood logs occupied we calculated the incidence-based frequencies per species, i.e., the number of occupied objects. Alpha and beta diversity were compared by considering the importance of the frequency of species along the Hill series. (**E**) We used the incidence-based frequencies to compare alpha and beta diversity between closed and open canopy conditions across succession. (**F**) We used generalized additive models (GAMs) and linear models (LMs) to test the effect of time on alpha diversity in interaction with the canopy treatment and the effect of time on the dissimilarity with time by Hill numbers.

National Park. The nomenclature followed MycoBank[48] and a complete species list is available in the Supplement (Table S1). During each field campaign, we estimated the stage of decomposition for each segment of the objects in four categories following Albrecht (1990)[49]. We then calculated the average decay stage per log based on the segments. Branches were treated as one segment. After 10 years, logs and branches were found in various decay stages, and some were already beginning to disintegrate (Figs. S1, S2).

Data preparation

To address our research questions, we calculated alpha and beta diversity (Fig. 1D). We used the incidence-frequency as basis, defined as the number of dead wood objects occupied by a species. We computed this measure for each canopy treatment and combinations of the tree species and dead-wood size. We calculated the incidence-frequency across blocks and also for each block separately. The data for each block were limited for some treatments. Still, the observed patterns were consistent with the overall approach (data not shown) even when spatial autocorrelation was included. We, therefore, present the results of the analyses across blocks here.

To address our research question, we additionally applied an approach based on Hill numbers[50]. The Hill framework allows the calculation of diversity indices based on the Hill number q, which gives increasing weight to the species frequencies[42] and has been used intensively for community ecological research[51–53]. $q = 0$ weights infrequent species based on incidence data and has been termed as "rare species", $q = 1$ weights frequently detected species and has been termed as "common species" and, $q = 2$ weights highly frequent species and has been termed as "dominant species".

To calculate the estimated alpha diversity of fungal fruiting communities, we used the function *iNEXT* within the R package 'iNEXT'[54]. This package provides diversity estimates based on rarefaction and extrapolation using incidence-frequencies. We used species richness ($q = 0$), the Shannon diversity index ($q = 1$)[55], and the Simpson diversity index ($q = 2$)[56]. We used dissimilarities as beta diversity measure. To analyze the dissimilarities between communities, we first estimated species similarity indices between open and closed canopies for each tree species and year using the *SimilarityPair* function within the R package 'SpadeR'[57]. To consider different similarity indices, we calculated the similarities of three Hill numbers: the Chao-Sørensen index ($q = 0$), the Horn index ($q = 1$), and the Morisita-Horn index ($q = 2$). Second, we calculated 1—estimated similarity values, to gain the dissimilarity of communities. The dissimilarity values range from 0 (equal communities) and 1 (completely different communities, meaning no shared species). Each estimate includes the 95% confidence interval based on 100 bootstraps. For a schematic overview of the variables used, please see Fig. 1D.

Statistical analysis

Alpha diversity

To test if treatment-based alpha diversity responded differently under closed and open canopies over time, we used generalized additive models (GAM, R package 'mgcv' function *gam*[58]). We used this approach to capture potential non-linear responses, which can be expected due to species accumulation[13,59]. Further, we did not include interactions between canopy and tree species, as we regarded tree species as replicates of the study. We additionally fit linear models (LMs). For an overview of the models fit, see Fig. 1F.

We first fit a model with the alpha diversity measures (q along the Hill series) as the response variable and factorial canopy openness and continuous time (years) as predictor variables. We used fewer knots ($k = 3$) for the smooth term, because the model did not converge with default values. Within a second GAM, we included an interaction term between time and canopy treatment to test for significantly divergent patterns between closed and open canopies over time. This can be achieved by a second GAM, which is specified as the first and adding the term "s(time, by = canopy)", which then gives a single estimate of the interaction term. We repeated this model for each tree species, wood size and Hill number (q) separately. A significant interaction would indicate differing slopes between closed and open canopies over time. However, a significant interaction can only inform of different slopes, not if single years are significantly different. Therefore, we also interpreted non-overlapping 95% confidence intervals as trends of differences between canopy treatments each year. Note that non-overlapping confidence intervals do not necessitate significance, so we interpret trends cautiously. We also used linear models (LM, R package 'stats' function *lm*), because many trends showed linear behavior and because testing interaction terms using LMs is more established than using GAMs[60]. We first fit a linear model with canopy treatment as a factor and time as a continuous predictor and a second model adding the interaction term of canopy and time. In both cases, GAM and LM, we used the fixed effects from the first model and the interaction term from the second model. We additionally inspected autocorrelation plots (R package 'stats' function *acf*) of the model residuals and did not observe signs of temporal autocorrelation, indicating no substantial influence of autocorrelation. Interpreting p-values from the first model with fixed effects and the second model with interaction effects would violate statistical principles, e.g., testing identical response and predictor variables in two models. Since our main interest was on the marginal effect of the canopy with time interaction, we only interpreted p-values for the interaction term.

Beta diversity

To test if dissimilarity between treatments changed over time, we used GAMs. We used dissimilarity as the response variable continuous time as the predictor variable. We further added the Hill series q as a grouping factor. We repeated the models for each tree species and wood size. The overall dissimilarity range of the slope was interpreted as the dissimilarity between closed and open canopies, with low dissimilarity for values < 0.5. Furthermore, we calculated a linear model and a posthoc test, using the R package 'stats' function *TukeyHSD*, to test if the pairwise dissimilarity means differ between dissimilarity estimates of rare, common and dominant

species. Where necessary, we applied Bonferroni corrections on the interpretation of p-values by considering significant only those below 0.016 due to multiple testing along the Hill series with three levels (i.e., 0.05/3).

To gain a further deeper understanding, (i) we reported overall species numbers associated uniquely with closed and open canopies to better understand differences in beta diversity between microclimate treatments. (ii) We showed the top two species that occurred either exclusively under closed or opened canopies or were found under both canopies. We also show their incidence-frequency over time. (iii) We prepared a table with the species exclusively found in either treatment and in time windows of two years to better understand the species that are most relevant for each treatment.

Ethics declarations

All national guidelines on species protection as well as the IUCN Declaration on Research on Endangered Species and the Convention on Trade in Endangered Species of Wild Fauna and Flora were complied within this study.

Results

We found 486 different fungal fruiting species across all dead wood logs and branches over a timespan of 10 years. On beech, we found 387 and on fir 307 species. On dead wood logs, we found 417 and on branches 304 species. In closed canopies, we found 397 species and under open canopies 363 species. Across years, we found up to ca. 25% of species uniquely in open, up to ca. 25% of species uniquely in closed canopies and more than ca. 50% in both microclimate treatments (Fig. 2). The species exclusive to either treatment are shown in Table 1.

We found an increasing treatment-based alpha diversity with time for logs and branches of both tree species (Fig. 3, Tables 2, 3). We did not find significant interactions between time and microclimate treatment (Tables 2, 3). However, temporal responses of fungal diversity differed when response trends and confidence intervals were considered: treatment-based alpha diversity of common and dominant species showed similar trends in the first

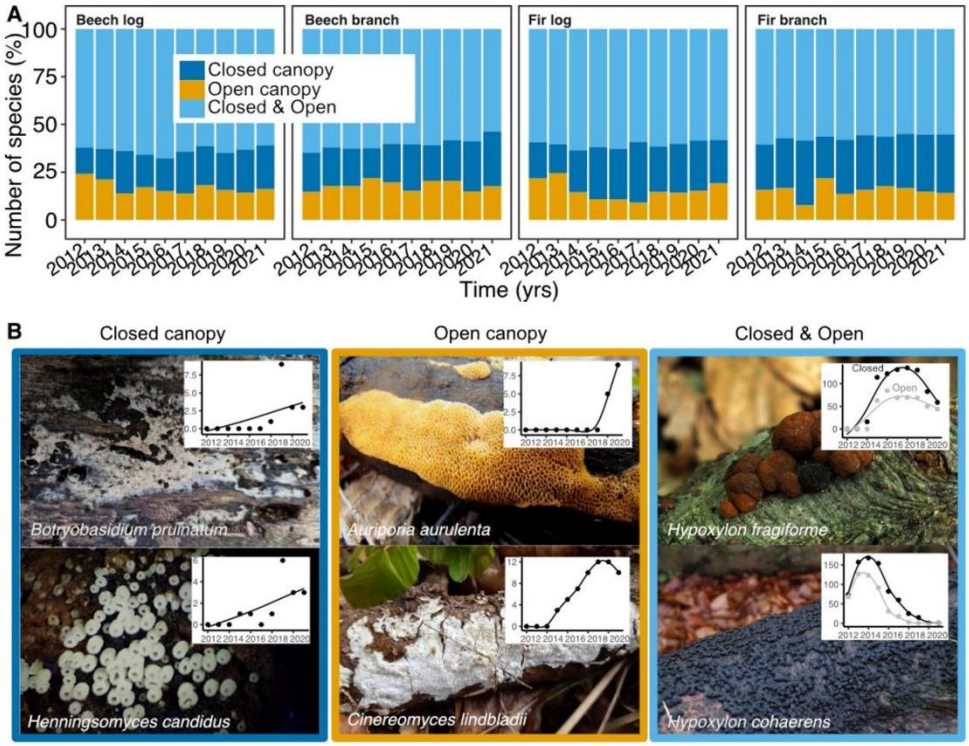

Figure 2. (**A**) The scaled number of species found shared and exclusively under the canopy treatments. (**B**) The most frequent two species occurring exclusively under closed, exclusively under open canopies and under both. Image credentials: *H. fragiforme* (Beech), *H. cohaerens* (Beech) and *H. candidus* (Fir) by Peter Karasch; *B. pruinatum* (Beech & Fir) by Jacob Heilmann-Clausen; *A. aurulenta* (Beech & Fir) by Joseba Castillo Munsuri and *C. lindbladii* (Beech & Fir) by gfiebes, both from iNaturalist. All images were used unaltered and were provided under CC BY-NC 4.0. Insets are incidence-frequencies over time with GAM smooth splines.

	Occurrence exclusively in years			
	1–2	3–4	5–6	7–8
Canopy treatment	Species	Species	Species	Species
Species exclusively fruited under open canopies	*Hymenoscyphus conscriptus*	*Ceriporiopsis gilvescens*	*Bisporella subpallida*	*Capitotricha bicolor*
	Lachnellula subtilissima	*Hypholoma marginatum*	*Capitotricha fagiseda*	*Dasyscypha nivea*
	Peniophora violaceolivida	*Hypochnicium wakefieldiae*	*Capronia pulcherrima*	*Galzinia incrustans*
	Pezicula cinnamomea	*Phanerochaete filamentosa*	*Durella macrospora*	*Hygrophoropsis aurantiaca*
	Phanerochaete raduloides	*Pluteus semibulbosus*	*Echinosphaeria canescens*	*Hypocrea protopulvinata*
	Sistotrema confluens	*Stereum rameale*	*Hyaloscypha britannica*	*Ischnoderma resinosum*
	Tylospora asterophora		*Hypochnicium geogenium*	*Kneiffiella barba-jovis*
	Valsaria insitiva		*Hypomyces aurantius*	*Lentomitella cirrhosa*
			Junghuhnia nitida	*Phlebia queletii*
			Phellinus ferruginosus	*Postia guttulata*
			Trechispora minima	*Psilocybe phyllogena*
			Tulasnella inclusa	*Sistotrema sernanderi*
				Thelephora atra
				Trametes multicolor
				Trechispora microspora
				Trechispora nivea
				Tremella obscura
				Trichophaea pseudogregaria
Species exclusively fruited under closed canopies	*Asterosporium hoffmannii*	*Auricularia auricula-judae*	*Colacogloea peniophorae*	*Athelia arachnoidea*
	Bulgaria inquinans	*Basidioradulum radula*	*Crepidotus versutus*	*Basidiodendron eyrei*
	Byssomerulius corium	*Flammulaster carpophilus*	*Entoloma cetratum*	*Botryobasidium aureum*
	Calycina discreta	*Hohenbuehelia atrocoerulea*	*Exidiopsis calcea*	*Byssocorticium caeruleum*
	Hyalorbilia berberidis	*Hohenbuehelia pinacearum*	*Flagelloscypha minutissima*	*Chaetosphaeria fusiformis*
	Hymenoscyphus scutula	*Melanomma sanguinarium*	*Herpotrichia macrotricha*	*Eriosphaeria aggregata*
	Sistotrema coroniferum	*Nectria cosmariospora*	*Hymenochaete cruenta*	*Flavophlebia sulfureoisabellina*
	Sistotrema efibulatum	*Olla scropulosa*	*Hyphodiscus hymeniophila*	*Gloeophyllum odoratum*
		Phaeohelotium trabinellum	*Kneiffiella microspora*	*Helminthosphaeria odontiae*
		Phlebia acerina	*Lachnum impudicum*	*Lachnum fasciculare*
		Unguicularia cirrhata	*Mycena zephirus*	*Leptosporomyces galzinii*
			Tulasnella pinicola	*Mycena metata*
			Tulasnella thelephorea	*Orbilia leucostigma*
				Pholiota limonella
				Psathyrella obtusata
				Pseudotomentella umbrina
				Simocybe coniophora

Table 1. Species exclusively found within closed and open treatments and in time windows of two years.

years but diverging trends in later years between microclimate treatments; in later years, common and dominant species showed lower alpha diversity trends in open canopies (Fig. 3). The responses were stronger for communities on fir than beech. Treatment-based alpha diversity of rare species showed almost non-distinguishable trends between closed and open canopies, with mainly overlapping confidence intervals (Fig. 3).

Communities on fir showed lower treatment-based alpha diversity in open compared to closed canopies throughout the succession, a trend which increased over time for common and dominant and remained constant for rare species (Fig. 3).

We found dissimilarity values of ca. 0.25 between microclimates on logs of both tree species and branches of beech (Fig. 4) and mostly non-significant trends of dissimilarity with time (Fig. 4, Table 4). We found higher dissimilarity values on fir branches, mainly for dominant and common species (Fig. 4). The average dissimilarity of rare species was significantly lower than that of common and dominant species (Fig. 4, Table 4).

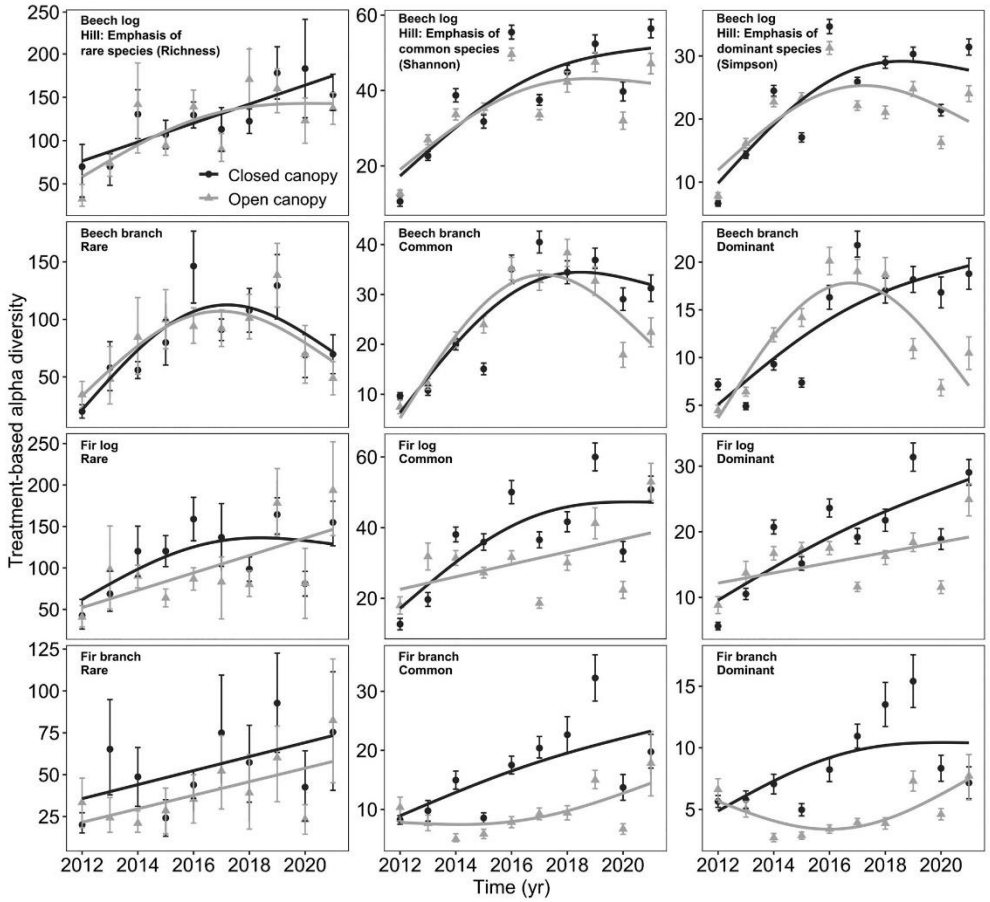

Figure 3. Treatment-based alpha diversity of fungal fruiting communities under closed (black) and open (grey) canopy treatments with time (years). Smooth splines are based on generalized additive models. Error bars are the 95% confidence intervals. For statistics, see Table 2.

Discussion

In this study, we used experimentally opened vs. closed forest canopies to contrast fungal treatment-based alpha and beta fruiting diversity across 10 years of dead-wood succession. Successional treatment-based alpha diversity patterns were mostly similar, with a trend towards lower richness under open canopies in later successional stages. We found moderate differences in dissimilarity between microclimate treatments that persisted over succession with up to ca. 25% of species uniquely associated with either microclimate treatment.

We found a trend towards lower richness in later years between the microclimate treatments, however, interaction terms were not significant. Further, we found that confidence intervals did not overlap in many cases, supporting the trend towards lower richness under open canopies in later years (Fig. 3). Thus, we did not find clear support for our first hypothesis but a trend following this expectation. Comparable studies using fungal treatment-based alpha diversity between canopy conditions are scarce, especially in a time series context. However, one study of the initial decay stage (first four years), using six tree species, found no significant alpha diversity differences between microclimate treatments among tree species[14]. The authors found no apparent differences in alpha diversity between canopy treatments for five of six tree species, including beech and fir. We also found no strong differences in the early decay stage. However, we found a trend towards differences in later years. This effect might become more robust and even more advanced in the decay stages in the following years. Thus, long time series under standardized conditions are necessary to illuminate diversity patterns.

			General additive model (GAM)					Linear model		
			Fixed	Smooth terms						
Tree	q	Predictor	t	edf	F	p	R2	t	p	R2
Beech	0 rare	Intercept	15.07				0.54	−4.72		0.53
		Canopy - open vs. closed	−0.78					−0.75		
		Time		1.60	15.73			4.75		
		Time x Canopy		2.04	1.39	0.290		−0.35	0.729	
	1 common	Intercept	15.81				0.56	−4.42		0.49
		Canopy - open vs. closed	−0.84					−0.72		
		Time		1.86	17.96			4.45		
		Time x Canopy		1.00	1.17	0.298		−0.86	0.404	
	2 dominant	Intercept	14.60				0.63	−2.81		0.26
		Canopy - open vs. closed	−1.12					−0.89		
		Time		1.91	10.87			2.83		
		Time x Canopy		1.00	2.69	0.123		−1.14	0.270	
Fir	0 rare	Intercept	9.94				0.44	−3.14		0.32
		Canopy - open vs. closed	−0.94					−0.94		
		Time		1.00	9.96			3.16		
		Time x Canopy		1.00	0.27	0.608		0.52	0.608	
	1 common	Intercept	11.88				0.32	−3.23		0.37
		Canopy - open vs. closed	−1.62					−1.62		
		Time		1.00	10.62			3.26		
		Time x Canopy		1.00	0.99	0.334		−1.00	0.334	
	2 dominant	Intercept	12.72				0.37	−3.71		0.44
		Canopy- open vs. closed	−1.79					−1.79		
		Time		1.00	13.93			3.73		
		Time x Canopy		1.00	3.15	0.095		−1.77	0.095	

Table 2. Statistics table for treatment-based alpha diversity in response to time and the canopy treatment for dead wood logs. We fit generalized additive models (GAM) and linear models. "Time x Canopy" denotes an interaction term. The alpha level is 0.016 (Bonferroni adjustment due to multiple comparisons). P values in brackets were not interpreted due to repeated testing. The abbreviations stand for: t = t-value, edf = effective degrees of freedom, F = F-value, $p = p$-value, R2 = R-squared.

One explanation for lower richness in later years might be that fruiting was reduced by the microclimatic conditions under open canopies, e.g., due to higher maximum temperatures and thus increased water loss, preventing from forming fruit bodies. Fungal fruiting is largely driven by macroclimate[58] and meteorological factors[61–64] often following a phase with high precipitation in summer and a cooling in fall[65] and can be delayed by drought[66]. With climate warming, fruiting, therefore, was observed to change towards longer fruiting seasons[65]. However, we have very limited knowledge available on the effects of experimental treatments on fruiting in real-world experiments. In the early phase, the same experiment as studied here, found that the species fruited under open conditions had tougher fruit bodies, likely to reduce water loss[45]. Adding to this, we here found only one species (*Hypholoma marginatum*) exclusively under open conditions that formed soft-fleshed mushrooms (pileate-stipitate fruit body). Further, this species fruited in the year 3–4, but no species exclusively under open conditions had such soft-fleshed fruiting bodies in later years (Table 1). In contrast, under closed conditions, we found five species that also fruited in later years such as *Entoloma cetratum*, *Mycena zephirus*, *Psathyrella obtusata*, *Pholiota limonella*, and *Simocybe coniophora* (Table 1). Thus, the fluctuating conditions under open canopies seem to be limiting for some species that produce fruit bodies with high water demand. However, further analyses are necessary to understand the adaptations and cues of fungal fruiting under variable microclimates. Another explanation might be that the species are lost from the substrates as mycelium due to unfavorable growth conditions and cannot be recorded in the fruiting record. We cannot disentangle these two explanations. This could be approached by estimating the presence of mycelium of species by metabarcoding or metatranscriptomes. Indeed, a series of publications have investigated metabarcoding of wood samples vs. fruit body-based sampling. How well above-ground reproductive structures in fungi can inform about below-ground mycelium is not entirely certain, especially across environmental gradients. Species prevalent with a high number of reads based on environmental sequencing approaches in deadwood also produced many fruit bodies[30]. However, this study also showed that some highly abundant species detected via sequencing could only rarely be found in the fruit body record. In another study, some rare fungal species could only be detected with fruit body sampling but not via environmental samples and metabarcoding[67]. Therefore, both approaches have limitations, and ideally, both are used jointly[68]. Nevertheless, fruit bodies are formed only when physiological and nutrient conditions of the mycelium and environmental conditions are suitable[69]. The fruiting community is likely a subset of the species

			General additive model (GAM)					Linear model		
			Fixed	Smooth terms						
Tree	q	Predictor	t	edf	F	p	R2	t	p	R2
Beech	0 rare	Intercept	12.74				0.63	−1.74		0.05
		Canopy - open vs. closed	−0.17					−0.11		
		Time		1.96	17.20			1.76		
		Time x Canopy		1.00	0.50	0.490		−0.43	0.670	
	1 common	Intercept	15.58				0.75	−3.32		0.33
		Canopy - open vs. closed	−0.79					−0.49		
		Time		1.97	28.04			3.34		
		Time x Canopy		1.51	3.02	0.162		−0.87	0.396	
	2 dominant	Intercept	11.16				0.53	−2.51		0.20
		Canopy - open vs. closed	−0.81					−0.62		
		Time		1.92	10.62			2.53		
		Time x Canopy		3.03	**8.23**	**0.005**		−1.65	0.119	
Fir	0 rare	Intercept	9.68				0.35	−2.94		0.35
		Canopy - open vs. closed	−1.86					−1.86		
		Time		1.00	8.79			2.96		
		Time x Canopy		1.00	0.00	0.959		−0.05	0.959	
	1 common	Intercept	10.67				0.48	−2.99		0.48
		Canopy - open vs. closed	−3.27					−3.27		
		Time		1.00	9.06			3.01		
		Time x Canopy		1.00	1.24	0.283		−1.11	0.283	
	2 dominant	Intercept	10.70				0.42	−2.02		0.42
		Canopy - open vs. closed	−3.39					−3.39		
		Time		1.00	4.17			2.04		
		Time x Canopy		3.26	**6.14**	**0.012**		−1.03	0.318	

Table 3. Statistics table for treatment-based alpha diversity in response to time and the canopy treatment for dead wood branches. We fit generalized additive models (GAM) and linear models. "Time x Canopy" denotes an interaction term. The alpha level is 0.016 (Bonferroni adjustment due to multiple comparisons). P values for fixed effects are not displayed due to repeated testing. The abbreviations stand for: t = t-value, edf = effective degrees of freedom, F = F-value, p = p-value, R2 = R-squared. Significant values are in [bold].

growing as vegetative mycelium, and it will be interesting in future studies to better understand why and under which conditions some produce fruit bodies and others do not. Nevertheless, the trend towards species loss or fruiting reduction in later years may indicate a change in successional trajectories.

However, even if the open canopy microclimate conditions are harsh and lead to a reduction of species, it is unclear why this would only happen in the later decay stages. One explanation might be based on the dominance-tolerance trade-off[39] and the characteristics of secondary colonizers. First, according to the dominance-tolerance trade-off, wood-inhabiting fungi either have narrow environmental tolerance but strong competitive abilities or vice versa. Second, first and secondary colonizers (those colonizing after endophytic fungi) require strong competitive abilities[70] and, therefore, might have low tolerance towards microclimatically fluctuating conditions. Taken together, colonizers in later decay stages may require increasingly competitive abilities to outcompete established species and may then have difficulties growing under open canopy conditions, which are characterized by variable conditions due to narrow tolerance. To test this hypothesis, manipulated fungal communities are required under steady vs. variable edaphic conditions.

It is a long-standing question whether environmental fluctuations lead to an increase or decrease in diversity[71,72]. Rapoport's rule, for example, predicts higher species ranges in northern areas[73], and one explanation is that species are more adapted to intense seasonality and thus are more tolerant towards changing conditions or fluctuations on smaller temporal scales as well. Indeed, a study on global soil fungi showed that species ranges are larger towards higher latitudes[36]. For fungi, a higher phylogenetic diversity was further found where thermal seasonality is stronger across Europe[74]. Across organism groups, fluctuating conditions in environmental variables can lead to variable responses, ranging from a decrease in diversity for planktons[75], increased diversity for bacteria[76] and increased diversity of wood-inhabiting fungi[77]. In later decay stages, we found a tendency towards lower diversity under open canopies (more fluctuating conditions) but not in early decay stages. A previous study used 16 fungal isolates within microcosms for 6 months and found an increase in species richness with increasing temperature fluctuation and suggested niche differentiation of the species as a mechanism for greater coexistence[77]. Thus, our results are partly in contrast with previous knowledge. The tendency towards lower diversity in later succession indicates that the effect of fluctuating microclimate differs across the succession and, thus, the number and composition of species. Therefore, to better understand the effects of environmental

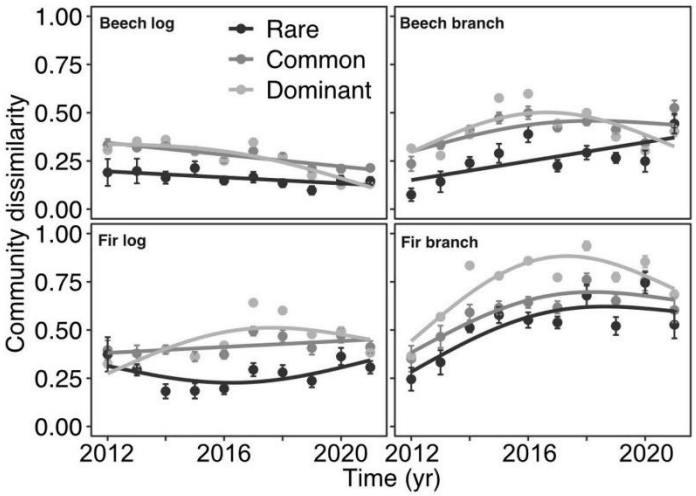

Figure 4. Treatment-based community dissimilarity of fungal communities between canopies with time (years). Smooth splines are based on generalized additive models. Error bars are the 95% confidence intervals. For statistics, see Table 3.

Predictor	Tree	q	edf	F	p	Tukey pairwise means			
						R2	Pair	t	p
Time (yr)	Beech log	0, rare	1.00	1.24	0.275	0.37	0–1	**4.09**	**0.001**
		1, common	1.00	4.76	0.038		0–2	**3.60**	**0.003**
		2, dominant	1.46	**8.37**	**0.005**		1–2	−0.49	0.878
	Fir log	0, rare	1.53	0.47	0.662	0.05	0–1	**3.99**	**0.001**
		1, common	1.00	0.48	0.494		0–2	**4.66**	**<0.001**
		2, dominant	2.20	2.01	0.110		1–2	0.67	0.782
Time (yr)	Beech branch	0, rare	1.00	1.24	0.275	0.37	0–1	**3.29**	**0.007**
		1, common	1.00	4.76	0.038		0–2	**3.44**	**0.005**
		2, dominant	1.46	**8.37**	**0.005**		1–2	0.15	0.988
	Fir branch	0, rare	1.54	3.07	0.048	0.05	0–1	1.26	0.428
		1, common	1.45	2.25	0.089		0–2	**3.36**	**0.006**
		2, dominant	2.14	3.90	0.030		1–2	2.10	0.109

Table 4. Statistics table for treatment-based community dissimilarity in response to time. We fit generalized additive models (GAM) and linear models. Using the Tukey posthoc test we tested for pairwise differences in means between diversity measures. The alpha level is 0.016 (Bonferroni adjustment due to multiple comparisons). The abbreviations stand for: t = t-value, edf = effective degrees of freedom, F = F-value, *p* = p-value, R2 = R-squared. Significant values are in [bold].

fluctuations based on canopy openness, an experiment could test how established communities react to sudden change from benign to fluctuating conditions, e.g., by community establishment under closed canopies with subsequent transfer to open conditions replicated across different decay stages. Further, our results from the temperate region might not apply to climates with more constant conditions, such as in humid tropics, and thus, replication of our experiment in such biomes would be important.

Our analyses further revealed that alpha diversity responded more strongly when common and dominant species were emphasized than when rare species were emphasized (Fig. 3). Thus, our results suggest that rare species may be more tolerant towards microclimatic fluctuations across succession. The Rapoports's rule might thus only apply to rare species. We also considered different tree species and wood sizes in our experiment. We found stronger divergence of common and dominant species in alpha diversity with time between canopies in branches than logs (Fig. 3). Two explanations may be possible: (i) a previous study found that logs and branches

harbor significantly different fungal fruiting communities when standardized for the surface area[13], which may respond more sensitive to open canopy conditions. (ii) The decomposition is faster within branches, and thus, the decay stage reached is already more advanced (Fig. S2), and later communities react stronger than earlier communities. Since we saw an increasing difference in alpha diversity with time within the logs it is reasonable to extrapolate further in time that effects may become more strongly in even later decay stages. Therefore, we hypothesize that communities associated with the third or fourth decay stage may be more sensitive to microclimatic fluctuations.

One alternative explanation for the reduced alpha diversity under open canopies may be differences in decay rates (successional speed) or moisture contents between dead wood in closed vs. open canopies. The decay under open canopies was found to be faster than under closed canopies[78–81]. However, one paper found no differences in the decomposition after 10 years of decay of logs between microclimates[23]. Thus we have inconclusive evidence whether decomposition increases, decreases or remains stable within different microclimates. Further, during decomposition the moisture content of dead wood increased[82,83], however, this was not studied yet in different microclimates. Nevertheless, differences in diversity between canopies might reflect differences in decay rates or moisture changes rather than succession (time). If true, we would expect no apparent differences in diversity patterns between canopies, when decay is the predictor instead of time. We found non-significant interactions between the decay stage and canopy treatment on alpha diversity (Fig. S3, Table S2) and no significant trends in beta diversity (Fig. S4, Table S3). However, although the interaction terms of the models were non-significant, we found non-overlapping confidence intervals and curve trends into different directions between microclimates for some years (Fig. S3). These results suggest either little differences in moisture content or decay stages between treatments or that species are little affected by them.

Finally, our study also contains limitations. First, the absence of a fruiting record cannot inform whether a species can grow as mycelium, but the presence provides information on which species can reproduce successfully. Second, we did not measure decay rates directly (e.g., mass loss[84]), but used a visual classification of dead wood objects using a four-classes system. We chose this approach because measuring decay rates via weighing is a destructive method and thus may disrupt succession. Further, visual decay classes are able to detect coarse differences in decomposition variation[85,86]. Third, our study does not capture the full successional trajectory. However, we cover the 10 years on the same objects, of which some reached decay stages three and four within this time frame (Fig. S2).

In conclusion, it is predicted that forest canopies will become increasingly opened up, and thus, potentially harsher microclimates will become more frequent[3]. Across succession, more fluctuating environments under open canopies only slightly affected species alpha diversity. However, we observed a trend towards a reduction of alpha diversity of common and dominant species in later decay stages. Under increasingly open conditions, late-decay fungi may experience difficulties in the future, which may also affect decomposition and humidification rates. Further, we found one-fourth of species fruiting exclusively under open canopies, and thus, open-canopy specialists may increase in population size. In summary, our study indicates that the fruiting of the fungal fruiting community on dead wood is currently rather resilient against the microclimatic fluctuations associated with the open canopy habitat and the predicted increase in canopy loss in temperate forests.

Data availability

The generated dataset that support the findings of this study is openly available in FIGSHARE https://figshare.com/s/7ace58d986dd8c8ff94f.

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Author contributions
CB, JM, PB and RB designed the concept of the study. JS, FSK and CB analysed, interpreted and wrote the manuscript. VB, HK and FR helped with the writing of the final manuscript.

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Competing interests
The authors declare no competing interests.

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"Effects of experimental canopy openness on wood-inhabiting fungal fruiting diversity across succession"

Supplementary Information

Figures

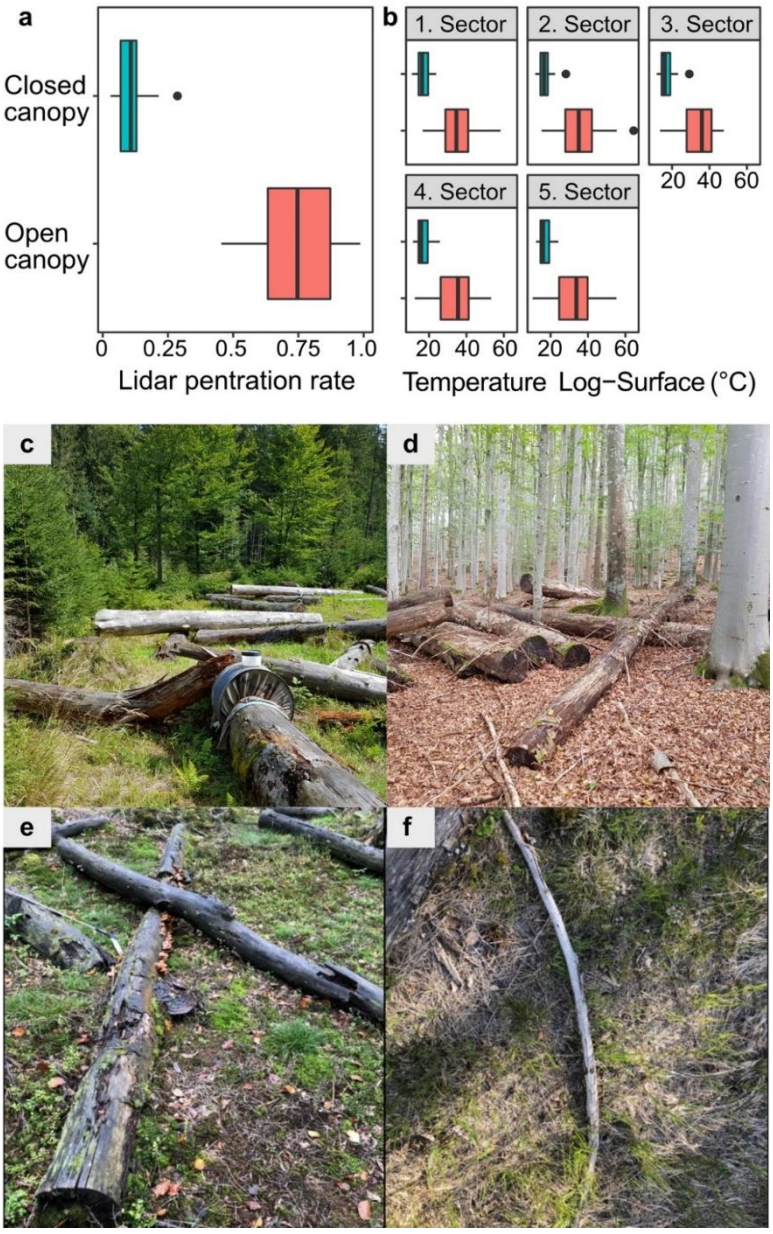

Figure S1 Demonstration of the microclimatic differences between closed (blue) and open canopies (red), based on a) LiDAR penetration rate, b) temperature measured on the surface of dead-wood logs on the same sunny day on a subset of the logs in the experiment for each of the five sectors on the log. c) Exemplary representative image of dead wood logs under opened

canopy treatment. Open canopy treatments are 0.1 ha clearings of all trees and shrubs. Further vegetation is mowed once per year to avoid shading by a dense grass layer surrounding the logs. On the image, this can be seen on the left side of the image border where a mowing edge is visible. d) Exemplary representative image of dead wood logs under the closed canopy treatment. e-f) Exemplary images of dead wood log and branch after 10 years of the experiment. Photos by Jasper Schreiber.

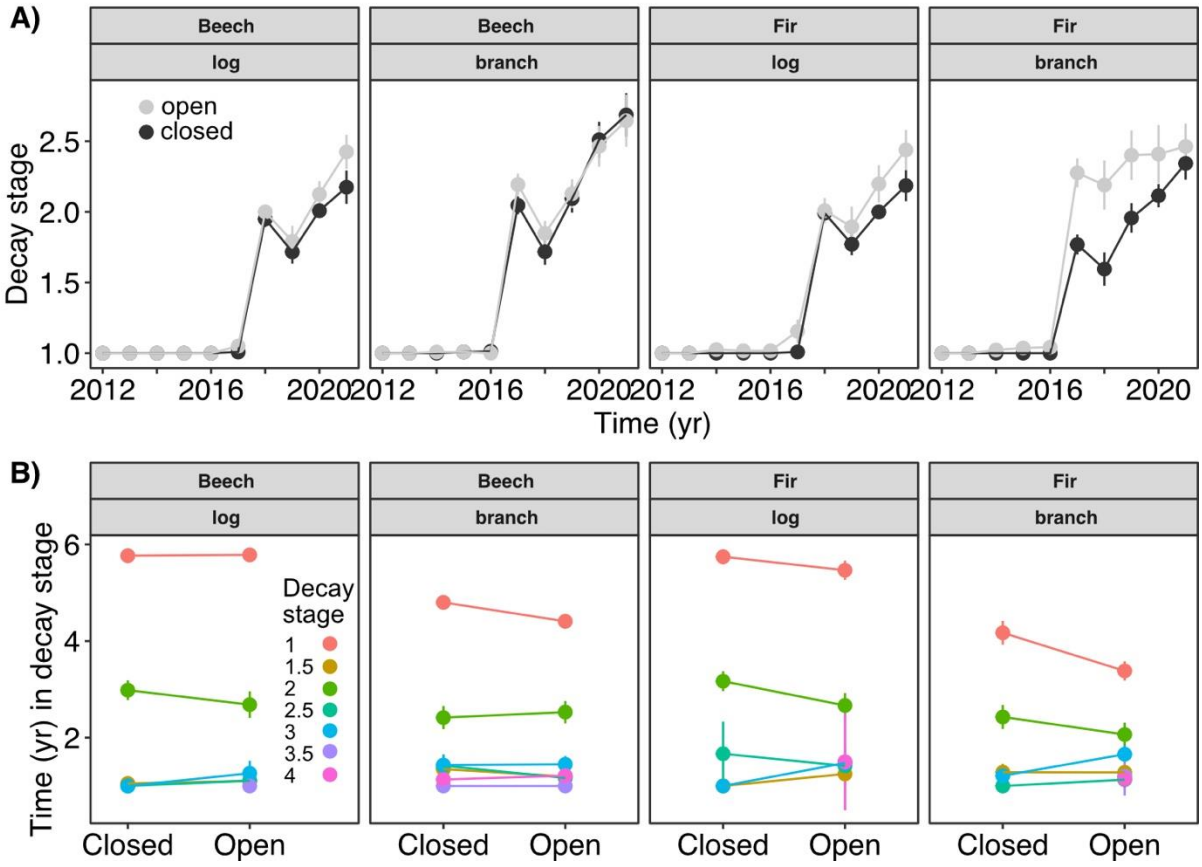

Figure S2 Decay stages of dead wood objects. A) Average decay stage of logs and branches in the years between canopy treatments. During each field campaign, we estimated the stage of decomposition for each segment of the objects (four categories according to (Albrecht 1990)). Each log was separated into seven segments. Each branch was treated as one sector. We then calculated the average decay stage per dead wood object based on the segments and then per year across objects. Please note the slight decrease in the decay stage in the year 2018 (branches) and 2019 (logs) is due to a different composition of recorders. B) Average time (years) a log or branch remains in a given decay stage. Data points are the means and error bars indicate double standard error.

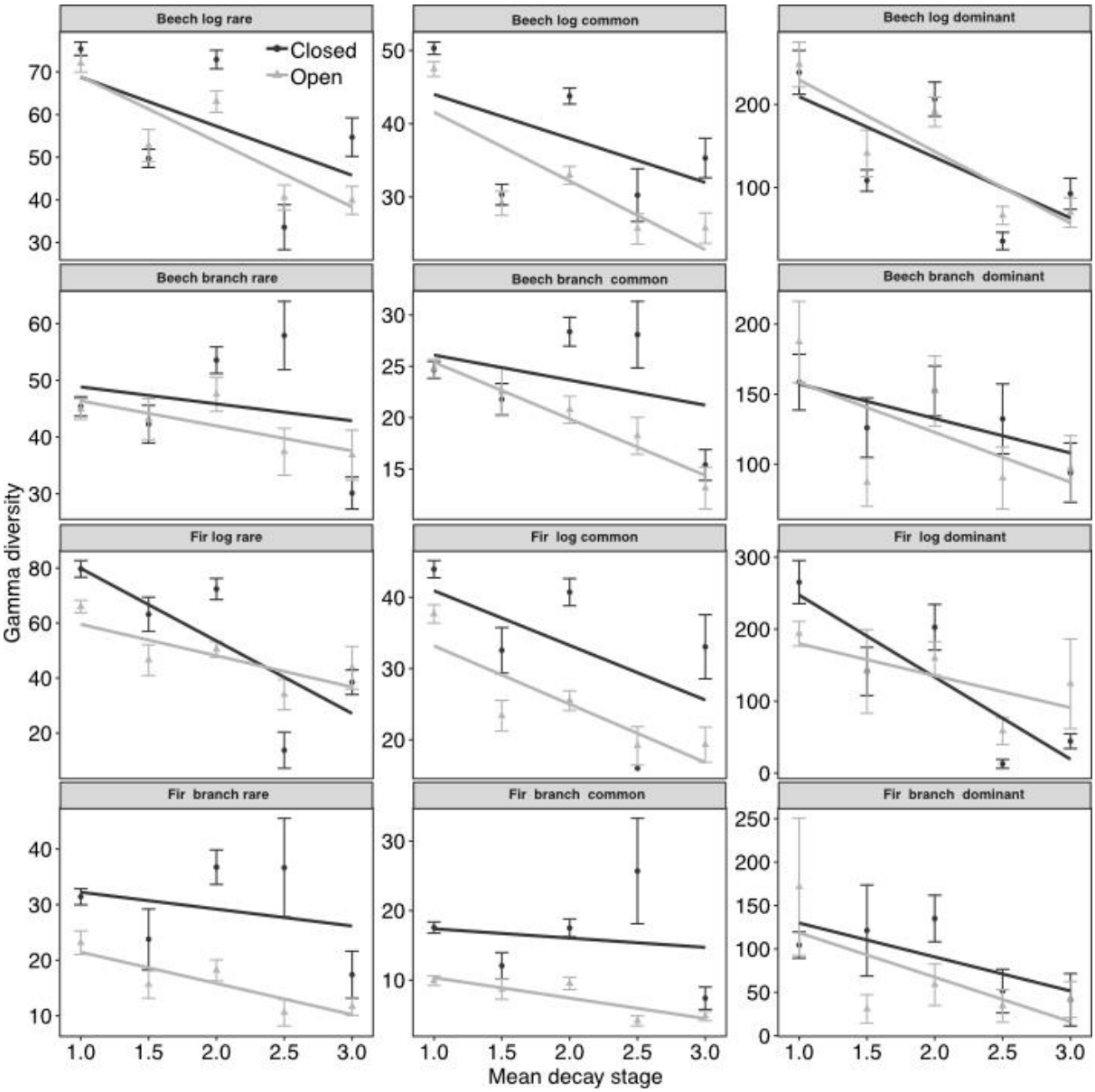

Figure S3 Gamma diversity of fungal fruiting communities under closed (black) and open (grey) canopy treatments with decay stages. The canopy treatments include closed and open canopy conditions for fungal growth. The estimated gamma diversity based on incidence-frequencies of three rare, common and dominant species using Hill numbers. Regression curves are based on linear models with continuous decay stage as predictor and gamma diversity as response variable. Error bars are the 95% confidence intervals. For statistics table see Table S2.

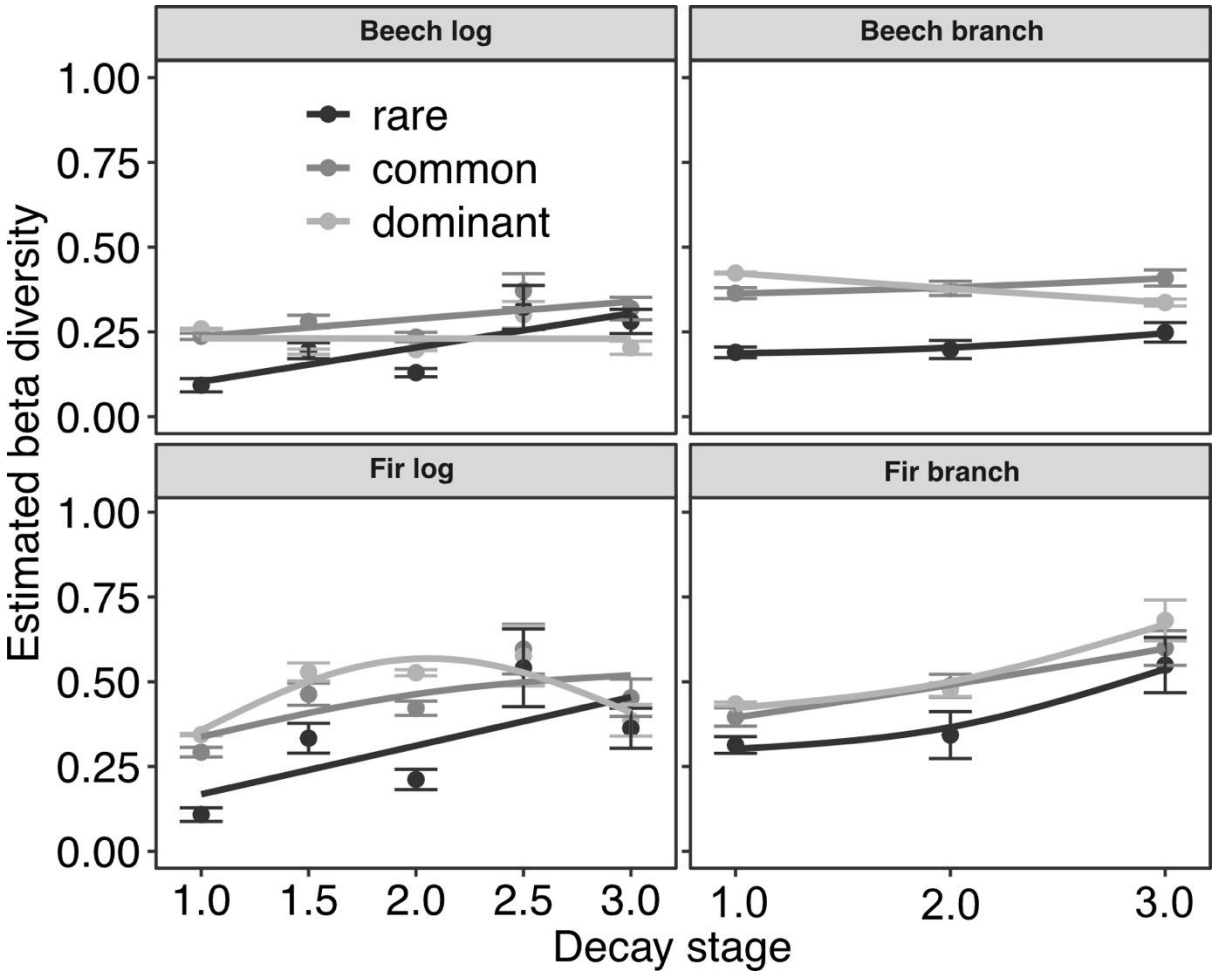

Figure S4 Beta diversity (dissimilarity) of fungal communities between canopy treatments with decay stages. The estimated beta diversity is based on incidence-frequencies of rare (q=0: Chao-Sørensen index, black line), common (q=1: Horn index, grey line) and dominant species (q=2: Morisita-Horn index, light grey line) using Hill numbers. Smooth splines are based on generalized additive models (GAM) with continuous decay stage as smoothed predictor and beta diversity as response variable. Error bars are the 95% confidence intervals.

Tables

Table S1 List of fruiting species of fungi and the number of colonized dead wood objects across 10 years of the experiment.

Species	Beech Closed branch	Beech Closed log	Beech Open branch	Beech Open log	Fir Closed branch	Fir Closed log	Fir Open branch	Fir Open log
Aleurodiscus amorphus	0	0	0	0	47	0	15	1
Alutaceodontia alutacea	0	0	1	0	0	1	0	2
Amphinema byssoides	0	0	0	1	1	0	0	2
Amylostereum chailletii	0	0	0	0	21	58	1	24
Antrodia heteromorpha	0	0	0	0	1	0	0	0
Antrodia serialis	0	0	0	2	0	1	0	3
Antrodia sinuosa	0	0	0	0	0	0	0	2
Antrodiella faginea	3	5	12	11	0	0	0	0
Antrodiella leucoxantha	0	0	0	1	0	0	0	0
Antrodiella onychoides	0	0	0	1	0	0	0	0
Antrodiella pallescens	0	0	0	1	0	0	0	0
Antrodiella romellii	0	0	1	0	0	0	0	0
Antrodiella semisupina	0	0	1	1	0	0	0	0
Antrodiella serpula	0	0	0	2	0	0	0	0
Aphanobasidium pseudotsugae	0	0	0	0	1	0	0	1
Armillaria gallica	0	3	0	0	0	0	0	1
Armillaria ostoyae	0	1	0	5	0	0	0	4
Ascocoryne cylichnium	0	17	1	14	0	4	0	2
Ascocoryne sarcoides	35	51	23	39	1	6	1	9
Ascocoryne solitaria	8	0	11	0	0	1	0	1
Ascodichaena rugosa	0	4	0	0	0	0	0	0
Ascotremella faginea	2	1	0	0	0	0	0	0
Asterosporium hoffmannii	0	2	0	0	0	0	0	0
Athelia arachnoidea	0	0	0	0	0	1	0	0
Athelia bombacina	0	0	0	0	0	1	1	1
Athelia decipiens	2	7	0	1	3	9	0	5
Athelia epiphylla	19	18	3	11	12	10	0	4
Athelia pyriformis	0	0	2	0	2	0	0	0
Auricularia auricula-judae	0	1	0	0	0	0	0	0
Auriporia aurulenta	0	0	0	3	0	0	0	9
Barbatosphaeria barbirostris	5	36	4	3	0	1	0	0
Basidiodendron caesiocinereum	0	1	1	0	0	1	0	0
Basidiodendron eyrei	0	1	0	0	0	2	0	0
Basidioradulum radula	0	0	0	0	0	1	0	0
Bertia latispora	0	0	1	0	10	19	2	1
Bertia moriformis	8	16	1	2	0	0	0	0
Biscogniauxia nummularia	0	1	0	0	0	0	0	0

Bispora antennata	5	55	4	51	0	5	0	2
Bisporella citrina	24	47	3	22	0	2	0	0
Bisporella pallescens	5	35	0	10	0	0	0	0
Bisporella subpallida	0	0	0	1	0	0	0	0
Bjerkandera adusta	0	47	0	45	0	11	1	35
Boidinia furfuracea	0	1	0	0	3	24	0	4
Botryobasidium aureum	2	0	0	0	0	0	0	0
Botryobasidium botryoideum	0	0	0	1	0	2	0	1
Botryobasidium botryosum	1	1	1	1	3	4	0	3
Botryobasidium candicans	0	1	2	2	6	5	0	6
Botryobasidium conspersum	3	8	2	4	0	0	0	2
Botryobasidium intertextum	1	0	0	0	0	0	0	2
Botryobasidium laeve	0	5	2	6	1	3	1	9
Botryobasidium medium	0	0	0	0	0	1	0	4
Botryobasidium obtusisporum	0	2	0	1	0	1	0	3
Botryobasidium pruinatum	3	6	0	0	0	2	0	0
Botryobasidium subcoronatum	15	19	2	10	9	29	0	11
Botryobasidium vagum	21	16	17	16	41	26	15	30
Botryohypochnus isabellinus	0	1	0	1	0	1	0	1
Brunnipila fuscescens	4	0	0	0	0	0	0	0
Bulgaria inquinans	0	1	0	0	0	0	0	0
Byssocorticium atrovirens	0	1	0	0	0	0	0	0
Byssocorticium caeruleum	1	0	0	0	0	0	0	0
Byssomerulius corium	1	0	0	0	0	0	0	0
Calocera cornea	32	58	39	57	2	2	0	2
Calocera furcata	0	1	0	0	22	21	4	33
Calocera viscosa	2	2	2	0	0	12	0	2
Calosphaeria pulchella	0	0	0	0	0	1	0	1
Calycina discreta	0	1	0	0	0	0	0	0
Calycina languida	0	7	0	0	0	1	0	0
Camarops lutea	0	1	0	0	0	0	0	0
Cantharellus tubaeformis	0	4	0	0	1	16	0	0
Capitotricha bicolor	0	0	4	0	0	0	0	0
Capitotricha fagiseda	0	0	2	0	0	0	0	0
Capronia pulcherrima	0	0	2	0	0	0	0	0
Catinella olivacea	0	1	0	0	0	0	0	0
Ceraceomyces eludens	0	0	0	0	0	1	0	0
Ceraceomyces serpens	2	4	0	3	2	1	0	0
Ceratobasidium cornigerum	0	1	0	0	0	2	0	2
Ceratostomella ampullasca	1	0	11	2	0	0	0	0
Ceratostomella rostrata	0	0	0	0	0	0	0	1
Ceriporia excelsa	0	2	2	0	0	0	0	0

Ceriporia viridans	1	1	0	2	0	0	0	0
Ceriporiopsis gilvescens	0	0	0	0	0	0	0	1
Chaetosphaeria fusiformis	0	0	0	0	1	0	0	0
Chaetosphaeria myriocarpa	1	1	1	0	0	3	1	0
Chaetosphaeria ovoidea	5	13	2	0	0	1	0	0
Chaetosphaeria pulviscula	2	0	1	0	1	0	0	0
Ciboria dumbirensis	1	0	0	1	0	0	0	0
Cinereomyces lindbladii	0	0	2	2	0	0	5	11
Cistella dentata	0	0	1	0	0	0	0	0
Claussenomyces atrovirens	2	5	0	1	0	1	0	0
Clitocybe ditopus	0	1	0	0	1	2	0	2
Clitopilus hobsonii	0	3	0	1	2	4	0	0
Colacogloea effusa	0	2	0	0	0	0	0	0
Colacogloea peniophorae	1	0	0	0	0	0	0	0
Coniochaeta spec.	2	5	12	25	1	5	6	14
Coniochaeta ligniaria	0	0	9	5	1	5	0	4
Coniochaeta malacotricha	0	0	5	1	6	6	7	18
Coniochaeta pulveracea	0	2	26	29	0	1	8	20
Coniochaeta subcorticalis	0	0	1	2	0	0	1	0
Coniochaeta velutina	0	1	62	46	0	4	4	16
Coniophora arida	0	1	0	1	0	0	6	1
Coniophora olivacea	0	0	0	0	0	2	1	3
Coprinus laanii	0	0	0	0	0	2	0	0
Coprinus micaceus	0	1	0	4	0	0	0	0
Coriolopsis gallica	0	0	0	2	0	0	0	0
Creopus gelatinosus	1	0	0	0	0	0	0	1
Crepidotus applanatus	0	0	0	0	0	0	0	1
Crepidotus cesatii	1	0	0	0	1	1	1	1
Crepidotus versutus	0	0	0	0	0	1	0	0
Cryptocoryneum condensatum	0	2	1	0	0	1	0	0
Cyanosporus alni	0	0	0	0	1	1	0	0
Cyathicula cyathoidea	0	0	2	1	0	0	0	0
Cylindrobasidium laeve	38	54	9	38	14	45	3	28
Dacrymyces capitatus	13	0	41	0	41	2	31	3
Dacrymyces stillatus	7	14	9	34	48	53	24	58
Dacrymyces tortus	0	0	0	0	1	3	0	0
Dacryobolus sudans	0	0	0	0	0	5	8	1
Dasyscypha nivea	0	0	1	0	0	0	0	0
Datronia mollis	3	19	0	7	0	0	0	1
Dematioscypha dematiicola	3	0	0	0	0	0	0	1
Dentipellis fragilis	0	6	0	3	0	0	0	1
Diatrype decorticata	23	4	33	8	0	0	0	0
Diatrype disciformis	64	37	31	7	0	0	0	0
Diatrype flavovirens	3	0	32	1	0	0	0	0
Diatrypella verrucaeformis	13	0	5	3	0	0	0	0
Durandiella gallica	0	0	0	0	8	1	8	0
Durella macrospora	0	0	0	2	0	0	0	0

Echinosphaeria canescens	0	0	1	0	0	0	0	0
Entoloma cetratum	0	0	0	0	1	0	0	0
Eriosphaeria aggregata	0	0	0	0	1	0	0	0
Eutypa spinosa	0	27	0	6	0	0	0	0
Eutypella quaternata	3	8	0	5	0	1	0	0
Exarmidium inclusum	1	2	14	58	4	4	34	36
Exidia pithya	0	0	0	1	25	21	1	28
Exidia plana	9	53	1	55	0	1	0	4
Exidiopsis calcea	0	0	0	0	0	1	0	0
Exidiopsis effusa	33	11	6	1	0	3	0	0
Flagelloscypha minutissima	0	0	0	0	1	0	0	0
Flammulaster carpophilus	0	0	0	0	0	1	0	0
Flammulaster limulata	0	0	1	0	0	0	0	0
Flavophlebia sulfureoisabellina	0	0	0	0	0	1	0	0
Fomes fomentarius	0	41	0	26	0	1	0	1
Fomitopsis pinicola	1	30	0	30	1	28	0	51
Fuscopostia fragilis	0	0	0	0	0	5	0	0
Galerina camerina	0	0	0	0	0	0	0	2
Galerina marginata	0	2	1	0	0	1	0	2
Galzinia incrustans	0	0	1	0	0	0	0	0
Ganoderma lipsiense	0	23	0	15	0	3	0	1
Gloeocystidiellum clavuligerum	1	1	0	0	0	0	0	0
Gloeocystidiellum luridum	1	0	0	0	0	0	0	0
Gloeocystidiellum porosum	1	2	0	0	1	0	0	1
Gloeophyllum odoratum	0	0	0	0	0	1	0	0
Gloeophyllum sepiarium	0	0	0	7	0	2	92	37
Grandinia aspera	1	2	0	2	2	9	0	7
Graphium calicioides	0	2	0	0	0	1	0	3
Gymnopilus sapineus	0	0	0	2	1	0	0	4
Gymnopus androsaceus	0	0	0	0	0	1	6	1
Gyromitra inflata	0	0	0	1	0	0	0	0
Hamatocanthoscypha laricionis	0	1	0	0	1	25	0	11
Helicogloea farinacea	0	2	0	0	0	1	0	0
Helicogloea lagerheimii	2	3	0	1	0	0	0	0
Helminthosphaeria odontiae	0	2	0	0	0	0	0	0
Helminthosphaeria stuppea	0	0	0	0	1	3	0	0
Henningsomyces candidus	0	0	0	0	2	7	0	0
Herpotrichia macrotricha	0	0	0	0	1	0	0	0
Heterobasidion abietinum	0	0	0	0	0	13	0	4
Heterobasidion annosum	0	0	0	0	0	13	0	6
Hohenbuehelia atrocoerulea	0	1	0	0	0	1	0	0
Hohenbuehelia pinacearum	0	0	0	0	1	0	0	0
Hyalorbilia berberidis	0	0	0	0	1	0	0	0
Hyalorbilia inflatula	11	4	5	2	3	2	0	1

Hyaloscypha albohyalina	7	0	0	0	0	0	0	0
Hyaloscypha aureliella	6	0	1	0	5	23	4	12
Hyaloscypha britannica	0	0	0	0	0	0	1	0
Hyaloscypha spiralis	26	6	7	1	1	1	1	0
Hygrophoropsis aurantiaca	0	0	0	0	0	0	0	1
Hymenochaete cruenta	0	0	0	0	1	0	0	0
Hymenoscyphus caudatus	0	0	0	1	1	0	1	0
Hymenoscyphus conscriptus	0	0	0	1	0	0	0	0
Hymenoscyphus scutula	0	0	0	0	0	1	0	0
Hymenoscyphus virgultorum	0	10	1	10	0	15	0	5
Hyphoderma argillaceum	4	6	2	1	0	4	0	0
Hyphoderma medioburiense	0	0	0	1	0	0	0	0
Hyphoderma mutatum	1	2	0	0	0	0	0	0
Hyphoderma obtusiforme	1	1	0	0	0	0	0	0
Hyphoderma praetermissum	16	27	5	18	5	19	1	6
Hyphoderma puberum	5	19	4	31	0	11	1	8
Hyphoderma roseocremeum	4	2	0	2	0	0	0	0
Hyphoderma setigerum	42	35	15	21	8	12	0	3
Hyphodiscus hemiamyloideus	3	7	0	4	0	0	0	0
Hyphodiscus hymeniophila	0	1	0	0	0	0	0	0
Hyphodontia alutaria	0	0	0	1	1	0	0	2
Hyphodontia arguta	0	0	0	1	0	0	0	1
Hyphodontia pallidula	0	0	0	4	0	3	0	5
Hypholoma capnoides	0	1	0	1	0	18	0	6
Hypholoma fasciculare	0	11	2	23	0	22	0	14
Hypholoma marginatum	0	0	0	0	0	0	0	1
Hypholoma subviride	0	1	0	1	0	0	0	0
Hypochnicium albostramineum	0	1	0	1	0	0	0	1
Hypochnicium bombycinum	0	1	0	1	0	0	0	0
Hypochnicium cremicolor	0	0	0	1	0	1	0	1
Hypochnicium eichleri	0	0	0	1	0	1	0	0
Hypochnicium erikssonii	0	3	0	2	0	0	0	2
Hypochnicium geogenium	0	0	0	0	0	0	0	1
Hypochnicium punctulatum	0	1	0	7	0	3	0	1
Hypochnicium subrigescens	0	6	0	4	0	1	0	3
Hypochnicium wakefieldiae	0	0	0	1	0	0	0	0
Hypocrea aureoviridis	0	1	0	0	2	1	0	0
Hypocrea citrina	0	4	0	4	0	2	0	0
Hypocrea protopulvinata	0	0	0	1	0	0	0	3
Hypocrea rufa	35	45	2	5	4	34	0	0
Hypomyces aurantius	0	0	0	1	0	0	0	0
Hypoxylon cohaerens	90	60	29	60	1	0	0	0

Hypoxylon fragiforme	113	60	79	60	0	0	0	0
Hypoxylon howeianum	0	0	0	2	0	0	0	0
Hypoxylon rubiginosum	44	57	33	41	0	0	0	0
Imleria badia	1	0	0	0	0	0	0	0
Inonotus hastifer	1	1	0	0	0	0	0	0
Inonotus nodulosus	3	9	1	2	0	0	0	0
Irpex lacteus	1	8	5	14	0	2	0	8
Ischnoderma benzoinum	0	0	0	2	0	5	0	3
Ischnoderma resinosum	0	0	0	1	0	0	0	0
Jaapia argillacea	0	0	0	0	0	0	0	1
Junghuhnia nitida	0	0	0	0	0	0	0	1
Kneiffia subalutacea	1	1	0	0	0	1	1	1
Kneiffiella abieticola	0	0	0	1	0	0	0	0
Kneiffiella barba-jovis	0	0	0	1	0	0	0	0
Kneiffiella microspora	1	0	0	0	0	0	0	0
Kretzschmaria deusta	1	9	0	1	0	0	0	0
Kuehneromyces mutabilis	0	3	0	0	0	3	0	0
Kurtia macedonica	2	0	0	0	0	0	0	0
Laccaria amethystea	2	1	0	0	2	6	0	0
Laccaria laccata	0	0	0	1	0	0	0	0
Lachnellula abietis	0	0	0	0	2	0	1	0
Lachnellula calyciformis	0	0	0	0	47	1	12	2
Lachnellula gallica	0	0	0	0	16	0	28	0
Lachnellula subtilissima	0	0	0	0	0	0	1	0
Lachnum fasciculare	1	0	0	0	0	0	0	0
Lachnum impudicum	1	0	0	0	0	0	0	0
Lachnum virgineum	7	1	20	1	0	0	0	0
Lactarius camphoratus	0	0	0	0	0	1	0	0
Lactarius helvus	1	1	0	0	1	1	0	0
Lactarius subdulcis	0	1	0	0	0	0	0	0
Lasiosphaeria canescens	0	0	4	1	1	4	0	1
Lasiosphaeria hirsuta	1	4	0	2	0	1	0	0
Lasiosphaeria ovina	2	12	0	5	0	0	0	0
Lasiosphaeria spermoides	1	6	1	5	0	1	0	0
Lasiosphaeria strigosa	3	3	7	3	3	23	0	6
Lawrynomyces capitatus	0	0	0	0	0	0	0	1
Laxitextum bicolor	19	17	5	10	1	1	0	0
Lentomitella cirrhosa	0	0	0	1	0	0	0	0
Lenzites betulinus	3	2	9	28	0	0	0	1
Leptodontidium trabinellum	4	4	0	0	0	0	0	0
Leptosporomyces galzinii	0	0	0	0	2	0	0	0
Leptosporomyces mutabilis	0	0	0	0	0	2	0	0
Leptosporomyces roseus	3	0	0	0	6	6	0	3
Leucoscypha leucotricha	1	0	0	0	0	3	0	0
Lopadostoma turgidum	7	0	2	0	0	0	0	0
Lopharia spadicea	0	1	4	2	1	0	0	0
Lophiotrema boreale	0	9	0	0	0	1	0	0

Lophium mytilinum	0	0	0	0	54	44	42	10
Lycoperdon perlatum	0	0	0	1	0	0	0	0
Lyomyces crustosus	0	0	2	0	0	2	0	0
Lyomyces sambuci	0	0	0	0	0	1	0	0
Melanomma pulvispyrius	33	59	30	24	2	20	1	4
Melanomma sanguinarium	0	1	0	0	0	0	0	0
Melanotus phillipsii	0	0	0	1	0	0	0	0
Merismodes anomalus	4	29	0	19	0	0	0	0
Metulodontia nivea	1	0	0	0	0	0	0	0
Mollisia aquosa	0	6	0	6	0	1	0	1
Mollisia fusca	7	0	4	3	0	0	0	0
Mollisia ligni	1	1	1	1	0	0	0	0
Mollisia lividofusca	1	4	7	7	0	0	0	0
Mollisia olivaceocinerea	100	60	110	54	1	9	2	6
Mucronella calva	0	2	0	0	0	9	0	6
Mycena abramsii	1	0	0	0	0	0	0	0
Mycena galericulata	0	1	0	3	0	0	0	0
Mycena galopus	1	0	0	1	0	0	0	1
Mycena haematopus	3	8	0	8	0	6	0	0
Mycena leptocephala	0	0	0	1	0	1	0	0
Mycena metata	0	0	0	0	2	0	0	0
Mycena pura	0	0	0	0	0	1	0	0
Mycena renati	0	3	0	0	0	0	0	0
Mycena rubromarginata	1	1	1	3	0	1	0	1
Mycena sanguinolenta	1	1	0	2	0	0	0	1
Mycena zephirus	0	0	0	0	0	1	0	0
Mycetinis alliaceus	0	1	0	0	0	0	0	0
Mycoacia nothofagi	0	2	0	2	0	0	0	0
Myxarium grilletii	0	3	2	1	0	0	0	0
Natantiella ligneola	0	1	2	1	0	4	1	3
Nectria cinnabarina	0	8	0	2	0	0	0	0
Nectria coccinea	38	58	15	23	3	3	0	0
Nectria cosmariospora	0	1	0	0	0	0	0	0
Nectria episphaeria	12	1	3	0	0	0	0	0
Nectria fuckeliana	0	0	0	0	25	28	7	4
Nectria magnusiana	2	1	1	0	0	0	0	0
Nectria peziza	0	0	0	0	0	1	0	1
Nemania chestersii	0	1	0	0	0	0	0	0
Nemania serpens	3	11	1	0	0	0	0	0
Nematogonum ferrugineum	0	1	0	2	0	4	0	0
Neobulgaria pura	43	30	3	5	0	0	0	0
Neodasyscypha cerina	7	58	4	41	0	0	0	0
Nidularia deformis	0	0	1	0	0	0	0	0
Olla scropulosa	1	0	0	0	0	0	0	0
Olla transiens	1	0	0	0	0	0	0	0
Ombrophila disciformis	2	5	1	4	1	0	0	0
Ombrophila janthina	0	2	0	4	0	0	0	0

Ombrophila violacea	1	1	0	0	0	0	0	0
Orbilia coccinella	1	2	0	0	0	0	0	0
Orbilia delicatula	61	59	11	59	5	48	2	28
Orbilia leucostigma	0	0	0	0	1	1	0	0
Orbilia sarraziniana	2	2	0	1	0	0	0	0
Oudemansiella mucida	0	6	0	3	0	0	0	0
Panellus mitis	0	0	0	1	6	18	1	5
Panellus serotinus	0	6	1	7	0	0	0	0
Panellus stypticus	0	11	0	4	0	0	0	0
Panellus violaceofulvus	1	1	0	0	5	27	0	5
Parorbiliopsis minuta	4	8	0	2	0	3	0	1
Patinella sanguineoatra	0	1	0	2	0	0	0	0
Paullicorticium pearsonii	0	0	0	0	1	0	0	0
Pellidiscus pallidus	0	0	0	0	5	0	0	0
Peniophora cinerea	11	25	20	46	0	2	1	3
Peniophora incarnata	3	8	1	15	0	4	0	1
Peniophora piceae	0	0	0	2	3	1	1	4
Peniophora pithya	0	0	0	1	6	5	17	1
Peniophora violaceolivida	0	0	0	1	0	0	0	0
Peniophorella pallida	1	0	1	0	0	3	0	1
Peniophorella tsugae	0	2	0	1	0	0	0	0
Pezicula acericola	1	4	1	0	0	1	0	0
Pezicula cinnamomea	0	0	1	0	0	0	0	0
Phaeohelotium carneum	2	0	0	0	0	1	0	0
Phaeohelotium trabinellum	0	1	0	0	0	0	0	0
Phanerochaete filamentosa	0	0	1	0	0	0	0	0
Phanerochaete galactites	1	1	1	0	0	0	1	0
Phanerochaete laevis	22	5	1	0	7	1	0	0
Phanerochaete leprosa	0	1	0	1	0	0	0	0
Phanerochaete livescens	32	9	1	1	1	1	0	0
Phanerochaete raduloides	0	0	1	0	0	0	0	0
Phanerochaete sanguinea	2	0	1	0	0	0	0	0
Phanerochaete sordida	21	5	11	2	30	7	4	1
Phanerochaete tuberculata	1	0	3	0	0	0	0	0
Phanerochaete velutina	17	13	0	1	1	2	0	0
Phellinus ferruginosus	0	0	1	0	0	0	0	0
Phellinus hartigii	0	0	0	0	0	1	0	0
Phlebia acerina	1	0	0	0	0	0	0	0
Phlebia lilascens	0	1	0	2	2	2	0	1
Phlebia livida	0	3	0	4	0	0	0	0
Phlebia queletii	0	0	0	0	0	0	0	1
Phlebia radiata	14	29	11	18	0	2	0	2
Phlebia rufa	12	13	2	8	0	0	0	0
Phlebia tremellosa	3	1	6	6	0	1	0	5
Phlebiella tulasnelloidea	0	3	1	0	0	2	0	0
Phlebiella vaga	28	10	5	1	7	13	6	2
Phlebiopsis gigantea	0	0	0	0	1	3	0	10
Pholiota cerifera	0	0	0	2	0	1	0	0

Pholiota lenta	0	1	0	1	0	3	0	0
Pholiota limonella	0	1	0	0	0	0	0	0
Pholiota tuberculosa	0	1	1	3	0	0	0	0
Physisporinus sanguinolentus	1	0	1	7	0	1	0	9
Physisporinus vitreus	0	0	0	1	0	0	0	0
Pleurotus ostreatus	0	5	0	6	0	1	0	0
Pleurotus pulmonarius	0	8	0	1	0	0	0	0
Plicaturopsis crispa	4	4	2	4	0	1	0	0
Pluteus cervinus	2	4	0	14	0	2	0	0
Pluteus semibulbosus	0	0	0	1	0	0	0	0
Polydesmia pruinosa	2	11	0	0	0	1	0	0
Polyporus brumalis	2	1	36	11	0	0	1	1
Polyporus ciliatus	0	0	8	1	0	0	0	0
Polyporus varius	1	1	0	2	0	0	0	0
Postia caesia	0	1	0	3	6	39	1	14
Postia guttulata	0	0	0	1	0	0	0	0
Postia stiptica	0	0	0	3	0	1	0	0
Postia subcaesia	0	11	1	2	1	0	0	0
Postia tephroleuca	0	24	1	19	0	3	0	4
Postia undosa	0	1	0	1	0	2	0	0
Proliferodiscus pulveraceus	0	1	0	0	0	0	0	0
Psathyrella obtusata	0	0	0	0	0	1	0	0
Psathyrella piluliformis	0	1	0	0	0	0	0	0
Pseudohydnum gelatinosum	0	0	0	0	0	2	0	0
Pseudotomentella tristis	1	0	0	0	0	0	0	0
Pseudotomentella umbrina	1	0	0	0	0	0	0	0
Psilocistella quercina	25	6	7	3	0	0	1	1
Psilocybe phyllogena	0	0	1	0	0	0	0	0
Pycnoporellus fulgens	0	2	0	2	0	6	0	30
Pycnoporus cinnabarinus	1	0	40	32	0	0	1	4
Radulomyces confluens	3	1	2	2	4	2	1	1
Resinicium bicolor	1	1	0	9	0	13	1	19
Resupinatus applicatus	0	0	2	2	0	0	0	0
Resupinatus trichotis	0	1	1	1	0	0	0	0
Rhodocollybia butyracea	0	1	0	0	0	0	0	0
Rigidoporus sanguinolentus	0	0	1	0	0	0	0	1
Rigidoporus vitreus	0	1	0	0	0	0	0	5
Rosellinia aquila	0	1	0	0	0	4	0	1
Rosellinia thelena	0	3	0	1	4	13	0	9
Russula mairei	0	0	0	0	0	4	0	0
Schizophyllum commune	9	1	74	57	0	1	19	20
Schizopora flavipora	0	0	0	0	0	2	0	1
Schizopora paradoxa	5	29	2	12	1	10	0	8
Schizopora radula	0	0	0	0	0	3	0	1
Scopuloides rimosa	0	0	0	2	0	0	0	0
Scutellinia cejpii	0	0	0	0	0	3	0	1

Scutellinia scutellata	0	1	0	0	0	2	0	0
Scutellinia subhirtella	0	1	0	0	0	3	0	0
Scutellinia umbrorum	0	0	0	0	0	2	0	1
Sebacina grisea	0	4	2	0	6	30	1	9
Sebacina incrustans	1	0	0	1	0	0	0	0
Serpula himantioides	0	0	0	0	0	2	0	1
Simocybe centunculus	0	6	1	2	0	0	0	0
Simocybe coniophora	0	1	0	0	0	0	0	0
Simocybe haustellaris	0	0	0	2	0	0	0	0
Sistotrema brinkmannii	27	25	38	23	9	21	4	21
Sistotrema confluens	0	0	0	0	0	0	0	1
Sistotrema coroniferum	0	0	0	0	1	0	0	0
Sistotrema diademiferum	0	0	2	0	0	1	0	0
Sistotrema efibulatum	0	0	0	0	1	0	0	0
Sistotrema oblongisporum	0	1	1	0	0	0	0	0
Sistotrema octosporum	1	0	3	0	0	0	1	2
Sistotrema porulosum	0	1	0	0	0	0	0	0
Sistotrema sernanderi	0	0	1	1	0	0	0	0
Sistotremastrum niveocremeum	3	0	5	0	0	1	0	0
Sistotremastrum suecicum	0	0	0	0	0	2	0	2
Skeletocutis amorpha	0	0	0	0	0	0	0	1
Skeletocutis carneogrisea	0	0	2	1	0	0	3	1
Skeletocutis nivea	1	2	2	3	0	0	0	0
Skvortzovia furfuracea	0	0	0	0	0	0	0	2
Sphaerobolus stellatus	0	0	7	0	0	0	2	0
Steccherinum ochraceum	0	3	0	0	0	0	0	2
Stereum hirsutum	36	56	18	53	0	0	0	0
Stereum rameale	0	0	1	0	0	0	0	0
Stereum rugosum	18	38	0	17	0	1	0	1
Stereum sanguinolentum	0	0	0	0	88	56	14	52
Stereum subtomentosum	2	2	0	0	0	0	0	0
Strossmayeria basitricha	4	0	0	0	0	0	0	0
Tapinella panuoides	0	0	0	0	0	1	0	0
Thelephora atra	0	0	0	0	0	0	0	1
Thelephora terrestris	68	19	30	22	58	33	29	28
Tomentella botryoides	2	2	0	0	0	0	0	0
Tomentella cinerascens	0	0	0	1	0	0	0	0
Tomentella lilacinogrisea	0	0	0	0	1	1	0	0
Tomentella sublilacina	0	0	0	1	0	1	0	0
Tomentella testaceogilva	0	1	0	0	0	0	0	0
Trametes gibbosa	0	21	0	27	0	0	0	1
Trametes hirsuta	11	11	83	59	0	1	3	12
Trametes multicolor	0	0	0	1	0	0	0	0
Trametes ochracea	0	3	0	4	0	0	0	0
Trametes versicolor	5	33	25	56	0	2	1	11
Trechispora cohaerens	0	0	0	1	0	1	0	0
Trechispora farinacea	0	3	1	2	1	0	1	1

Trechispora hymenocystis	6	1	0	3	1	6	0	7
Trechispora microspora	0	0	0	0	0	0	1	0
Trechispora minima	0	0	0	0	0	0	1	0
Trechispora mollusca	4	0	0	1	0	2	0	2
Trechispora nivea	0	0	0	0	0	0	1	0
Tremella encephala	0	0	0	0	3	0	0	0
Tremella foliacea	3	7	1	0	0	0	0	2
Tremella obscura	0	0	0	0	0	0	1	0
Trichaptum abietinum	0	0	0	0	2	5	1	10
Trichaptum biforme	0	0	0	1	0	0	0	0
Tricholomopsis decora	0	0	0	2	0	0	0	2
Tricholomopsis rutilans	0	0	0	0	0	2	0	0
Trichophaea pseudogregaria	0	0	0	0	0	0	0	1
Tromeropsis microtheca	0	4	6	22	0	4	21	52
Tubeufia cerea	1	2	6	0	0	0	0	0
Tubulicrinis strangulatus	0	0	0	0	0	0	0	1
Tubulicrinis subulatus	0	0	0	0	0	0	0	1
Tulasnella eichleriana	3	5	2	1	0	5	0	1
Tulasnella inclusa	0	0	1	0	0	0	0	0
Tulasnella pinicola	0	1	0	0	0	0	0	0
Tulasnella pruinosa	3	0	0	0	0	0	0	0
Tulasnella thelephorea	1	0	0	0	0	0	0	0
Tulasnella violacea	0	1	1	0	0	0	0	0
Tulasnella violea	5	12	6	1	0	1	1	0
Tylospora asterophora	0	0	0	0	0	0	0	1
Tylospora fibrillosa	2	1	0	0	2	2	0	0
Tympanis hypopodia	0	0	0	0	0	1	1	2
Typhula erythropus	0	2	0	1	0	2	0	1
Typhula setipes	0	0	0	0	0	6	0	5
Unguicularia cirrhata	0	2	0	0	0	0	0	0
Valsaria insitiva	0	0	1	13	0	0	0	0
Xenasmatella ardosiaca	0	1	0	0	0	0	0	0
Xenasmatella fibrillosa	0	0	0	1	0	0	0	0
Xylaria hypoxylon	4	28	0	5	0	0	0	0
Xylaria polymorpha	0	2	0	0	0	0	0	0
Xylodon brevisetus	0	0	2	0	1	5	0	6
Xylodon nespori	0	2	1	1	1	8	0	1
Xylodon rimosissimus	0	0	0	1	0	0	0	0
Xylodon spathulatus	0	8	0	6	0	20	0	13

Table S2 Statistics table for gamma diversity in response to decay stage and the canopy treatment for dead wood logs and branches. We fit linear models with gamma diversity as response and factorial canopy treatment, continuous decay stage and their interaction term as predictors. Alpha level is 0.016 (Bonferroni adjustment due to multiple comparisons). P values for fixed effects are not displayed due to repeated testing. The abbreviations stand for: t= t-value, edf= effective degrees of freedom, p= p-value.

		Logs			Branches		
q	**Predictor**	**t**	**p**	**R^2**	**t**	**p**	**R^2**
0 rare	Intercept	6,75		0,31	6,40		0,06
	Canopy - open vs. closed	-0,46			-0,74		
	Time	-2,40			-0,99		
	Time x Canopy	-0,32	0,762		-0,18	0,865	
1 common	Intercept	7,64		0,39	7,79		0,35
	Canopy - open vs. closed	-1,31			-1,47		
	Time	-2,46			-2,19		
	Time x Canopy	-0,51	0,627		-0,83	0,440	
2 dominant	Intercept	5,38		0,49	6,52		0,28
	Canopy - open vs. closed	0,20			-0,53		
	Time	-3,24			-2,27		
	Time x Canopy	-0,25	0,811		-0,39	0,712	
0 rare	Intercept	5,85		0,39	5,81		0,54
	Canopy - open vs. closed	-0,55			-3,25		
	Time	-2,71			-1,49		
	Time x Canopy	1,09	0,319		-0,42	0,692	
1 common	Intercept	6,63		0,43	3,85		0,38
	Canopy - open vs. closed	-1,76			-2,59		
	Time	-2,39			-0,91		
	Time x Canopy	-0,07	0,944		-0,32	0,762	
2 dominant	Intercept	5,05		0,45	4,60		0,38
	Canopy - open vs. closed	0,06			-0,94		
	Time	-3,07			-2,56		
	Time x Canopy	1,45	0,198		-0,32	0,760	

Table S3 Statistics table for beta diversity in response to decay stages. We fit generalized additive models (GAM) and linear models. Using Tukey post-hoc test we tested for pairwise differences in means between diversity measures. Alpha level is 0.016 (Bonferroni adjustment due to multiple comparisons). The abbreviations stand for: edf= effective degrees of freedom, F=F-value, p= p-value.

							Tukey pairwise means		
Predictor	**Tree**	**q**	**edf**	**F**	**p**	**R^2**	**Pair**	**t**	**p**
Decay stage	Beech log	0, rare	1.00	5.92	0.033	0.24	0-1	1.88	0.185
		1, common	1.00	1.51	0.245		0-2	0.59	0.829
		2, dominant	1.00	0.00	0.989		1-2	-1.30	0.424
	Fir log	0, rare	1.00	3.18	0.105	0.05	0-1	1.66	0.259
		1, common	1.00	1.27	0.285		0-2	2.00	0.155
		2, dominant	1.52	0.41	0.596		1-2	0.34	0.940
Decay stage	Beech branch	0, rare	1.00	1.24	0.275	0.24	0-1	**6.22**	**0.002**
		1, common	1.00	4.76	0.038		0-2	**6.04**	**0.002**
		2, dominant	1.46	**8.37**	**0.005**		1-2	-0.18	0.983
	Fir branch	0, rare	1.00	3.84	0.107	0.05	0-1	0.93	0.640
		1, common	1.00	2.86	0.152		0-2	1.30	0.445
		2, dominant	1.00	4.19	0.096		1-2	0.37	0.930

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10.3 Fungal fruit body assemblages are tougher in harsh microclimates

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Fungal fruit body assemblages are tougher in harsh microclimates

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Forest species are affected by macroclimate, however, the microclimatic variability can be more extreme and change through climate change. Fungal fruiting community composition was affected by microclimatic differences. Here we ask whether differences in the fruiting community can be explained by morphological traits of the fruit body, which may help endure harsh conditions. We used a dead wood experiment and macrofungal fruit body size, color, and toughness. We exposed logs of two host tree species under closed and experimentally opened forest canopies in a random-block design for four years and identified all visible fruit bodies of two fungal lineages (Basidio- and Ascomycota). We found a consistently higher proportion of tough-fleshed species in harsher microclimates under open canopies. Although significant, responses of community fruit body size and color lightness were inconsistent across lineages. We suggest the toughness-protection hypothesis, stating that tough-fleshed fruit bodies protect from microclimatic extremes by reducing dehydration. Our study suggests that the predicted increase of microclimatic harshness with climate change will likely decrease the presence of soft-fleshed fruit bodies. Whether harsh microclimates also affect the mycelium of macrofungi with different fruit body morphology would complement our findings and increase predictability under climate change.

Analyses of functional traits help to better understand and predict species community change in response to environmental change[1,2]. Organism body size, color, or toughness are important traits related to the thermal climate. Climate warming has already decreased body size and increased light-colored communities[3,4]. Besides the average annual temperature increase, forest organisms experience heterogeneous microclimatic conditions, e.g., because of canopy cover change[5,6]. Open forest stands are characterized by extreme temperatures and radiation[7–10], which can even exceed macroclimatic mean differences[6,8] (hereafter "harsh microclimate"). Closed canopies, in contrast, buffer these extremes[8,11]. Forest management activities, natural disturbances, and climate change increase canopy loss, leading to harsher microclimates[12–15]. Previous studies showed that many forest species groups differ in community composition between closed and open canopies[16,17]. Although fungal fruiting communities were previously found to differ between microclimates[17,18], we currently do not know if fruit body traits differ as well.

Fungi are ectotherm, and modular organisms, characterized by a mycelium (consisting of hyphae), and many species produce multicellular fruit bodies (hereafter "macrofungi") for sexual reproduction and the subsequent development of spores[19]. Mycelium grows within the substrate, e.g., soil or dead wood, exploiting resources (e.g., decay of organic matter)[20]. Before fruiting, the mycelium must reach a critical size (e.g., biomass) with a critical amount of storage mycelium, which serves fruit body production[21,22]. Before maturation, fruiting cues start the fructification process by forming fruiting body initials, primordia, maturating fruit bodies, and finally mature fruit bodies with sexual spores[22,23]. Species that can successfully grow as mycelium and form mature fruit bodies in a given environment must endure the below- and above-ground conditions. Both modules have evolved strategies to cope with stressful conditions[24,25]. The presence of a fruit body in an environment requires biochemical[25] and morphological adaptations of the fruit body[26–29]. Several studies provided evidence that fruit body traits are under selection[30–32] and can function to tolerate harsh climate conditions[33,34]. However, whether the presence of morphological traits of the fruit body is related to the microclimate is currently unknown. We thus expect non-random fruit body trait distribution with microclimates, which would imply morphological features of the fruit bodies that enhance their survival. The absence of fruit bodies, however, may be the result of multiple

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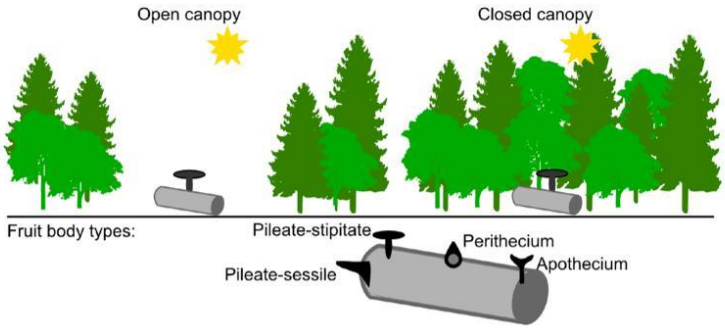

Figure 1. Conceptual representation of the study treatment and fruit body types. Random block design with five blocks, each with 12 plots with open and 12 with a closed canopy. Forest stands with open canopies are characterized by direct sun exposure and thus increased radiation, heat, and drought ("harsh microclimate"), compared with forest stands with closed canopies[7,11]. We investigated trait change of four fruit body types: pileate-stipitate and pileate-sessile for Basidiomycota and Perithecia and Apothecia for Ascomycota. Illustration by F.-S. Krah.

processes. First, the environment does not allow a species to grow as mycelium, and hence fruit bodies are also absent. Second, a species grows as mycelium within the environment, but fruit body production is absent (e.g., because a minimal storage-mycelium necessary to produce fruiting structures could not be formed[21]). Third, a species grows as mycelium within the environment, but production of fruit bodies is prohibited, e.g., absence of fruiting cues or physiological damage during growth of primordia, growth of fruit bodies, and after maturation.

We currently have little understanding of which fruit body traits may be related to harsh microclimates. Two macroecological studies demonstrated that fruit body size and color lightness are correlated with the climate on a large spatial scale[26,27]. European fruiting communities were darker in cold environments, possibly as an adaptation to increase fruit body temperature and thus improve spore production[26]. On a global scale, fruiting communities had smaller fruit bodies in hot or cold environments, possibly an adaptation for cooling down or heating more rapidly[27]. Further, one study tested the effect of forest edges (characterized by sun exposure) on fruit body morphology and found a higher richness of hard-fleshed, long-lived fruit bodies at the forest edge[29]. Taking these results together, fruit body morphology may allow the fruit body to endure harsh conditions, such as temperature variability or UV radiation[33,35]. However, whether morphological traits of the fruit body show pattern that might explain differences in the fruiting communities between microclimates has not been tested.

If fruit body size, color lightness, and toughness are related to harsh microclimate conditions as outlined above, the following responses of the fruiting community can be expected: (1) based on considerations of the surface-area-to-volume ratio, one might expect larger or smaller fruit bodies in harsh microclimates. Larger fruit bodies have higher thermal inertia, whereas smaller ones can get rid of excess heat faster ('heat conservation hypothesis'[36], and 'heat-up-cool-down-hypothesis'[27]). Both may potentially lower heat stress under open canopies. (2) Based on considerations of the pigmentation of fruit bodies, one might expect more bright- or dark-colored fruit bodies in harsh microclimates. Strong pigmentation of fruit bodies may lower the damaging effect of radiation and desiccation under open canopies, because melanin pigmentation reduces oxidative stress ('melanism-desiccation hypothesis'[37] and 'photo-protection hypothesis'[38]). Weak pigmentation may reduce heat stress, which increases with increasingly darker fruit bodies ('thermal-melanism hypothesis'[26,39]). (3) Based on considerations of the toughness of fruit bodies, one might expect more tough-fleshed fruit bodies in harsh microclimates. The toughness of the fruit body may lower heat and desiccation stress by reducing the transpiration rate ('toughness-protection hypothesis'). Here we thus test the pattern of community traits that might result from different processes described by these hypotheses.

We used a dead-wood experiment on a landscape scale and manipulated dead-wood logs of two tree species under closed canopies and experimentally created forest gaps (0.1 ha, hereafter "open canopies", Fig. 1). Fungal fruiting communities were assessed via fruit body-based inventories across four years of the initial phase of decomposition and 320 dead-wood logs of the same size. We assembled trait data of fruit body size from literature, fruit body color lightness from photographs, and classified fungi into soft- and tough-fleshed (toughness) based on expert knowledge. We calculated fungal fruiting community traits for presence/absence data, and we further applied a null model to test against a random distribution of species in the microclimates to approach our expectations. Here we address the overall question of whether fruit body size, color and toughness of communities are related to microclimate harshness.

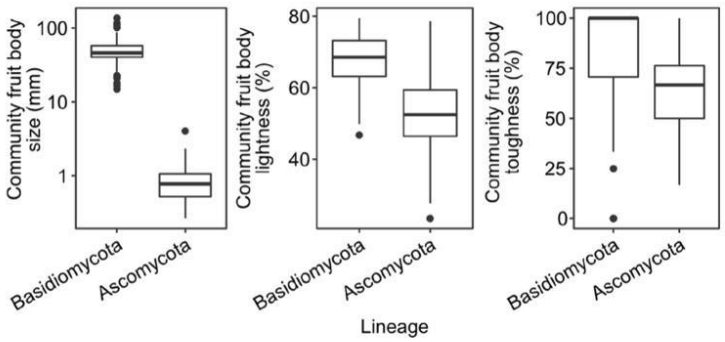

Figure 2. Differences in community fruit body traits between lineages. Note that fruit body size is $\log_{10}$-transformed. We used linear mixed-effects models with a nested random effect on block and plot to test for significance. Statistics values are given in the text. R programming environment version 4.1.2[40] and R add-on package *ggplot2*[41].

Results

We found significantly larger (LME: z value = − 67.00, $p < 0.001$) and more tough-fleshed fruit bodies (LME: z value = − 5.11, $p < 0.001$) for Basidiomycota compared with Ascomycota (Fig. 2). Community fruit body lightness was also higher in Basidio- compared with Ascomycota, but not significantly (LME: z value = 1.73, $p = 0.083$, Fig. 2).

We then tested for responses of the fruiting community traits with canopy openness. In the overall model (across lineages and tree species), we found significantly larger fruit bodies under open canopies ($z = 5.79$, $p < 0.001$, Fig. 3; Table 1). Fruit body size, however, differed in response between lineages (Fig. 3; Table 1). Basidiomycota communities showed significantly larger ($z = 3.35$, $p < 0.001$), Ascomycota communities significantly smaller fruit bodies under open canopies ($z = -4.62$, $p < 0.001$; Figs. 2, 3; Table 1). Whereas we found opposing effects between the two tree species within Basidiomycota, we found consistent effects within Ascomycota (Fig. 3; Table 1). Fruit body color lightness was significant in only one model. Basidiomycota communities showed significantly lighter fruit bodies under open canopies on beech dead wood (Fig. 3; Table 1). Further, we found a significantly higher proportion of tough-fleshed fruit bodies under open canopies ($z = 10.22$, $p < 0.001$; Fig. 3; Table 1), which was significant across lineages and tree species (Fig. 3; Table 1).

We used a null model to test against a random draw of species in plots. We found consistent responses of the SES community traits of the observed and the standardized community traits (Fig. 4, Table 1).

We further tested the effects of the canopy on all traits in one model using generalized linear models (GLM). The GLM allowed comparing effect sizes between the community traits within one model. The results of the GLMs were largely consistent with the results based on the LMEs (Table S3). Fruit body toughness ($z = 7.65$) showed the largest relative effect size compared to community fruit body size ($z = 5.23$) and lightness ($z = -0.41$; Table S3).

Discussion

We found a significant increase in fruiting community toughness with canopy openness and toughness responded most strongly with canopy openness compared with community fruit body size or color lightness. Together, these results suggest that morphological traits of the fruit body at least partly explain previously observed shifts in the fruiting community between microclimates.

Fruit body toughness has not yet been considered directly as a variable. Although toughness was not directly used as a variable in a previous study, soft-fleshed (agaricoid) richness was negative, tough-fleshed (polyporoid) richness of wood-inhabiting fungi was positively affected by forest edges[29]. Like open canopies, forest edges are also characterized by higher sun exposure. Thus, these results are consistent with our findings. Further, an increase in tough-fleshed species was suggested in areas with a pronounced drought season in West Africa[42]. Experimental studies are rare, however, tough-fleshed fruit bodies may provide desiccation protection due to the enhanced stability of the fruit body towards water loss due to either denser hyphal system and thicker cell walls[33]. One experiment found that cell layers with dense cell structures have a lower transpiration rate, but this was tested based on a few species, only[43]. Protection mechanisms against desiccation via a reduction in water loss is a well-known adaption of plants in dry environments. For example, Mediterranean ecosystems are characterized by sclerophyll vegetation with hard leaves[44,45]. More specifically, the olive tree, as a typical Mediterranean plant species, shows strong drought/heat adaptation. Besides lowering water content and water potential in tissues, the olive tree developed morphological adaptations such as thick leaf cuticle and waxy substances, hairiness of the leaf abaxial surface, or high specific weight of leaves[46]. Those adaptations can reduce water loss and thus increase the fitness of the plant[46]. Furthermore, a meta-analysis investigated the dry leaf mass per unit

	Size (OBS/SES)	Lightness (OBS/SES)	Toughness (OBS/SES)
Intercept	7.41***/− 1.66	− 25.36***/1.16	**6.33*****/− **4.39*****
Canopy openness—open	**5.79*****/**6.45*****	− 0.92/− 0.54	**10.22*****/**13.21*****
Tree species	− 1.70/− 3.55***	− 0.78/− 1.10	1.60/− 1.25
Size		**6.16*****/**6.09*****	0.04/− 0.83
Lightness	**6.11*****/**6.03*****		1.06/1.34
Toughness	0.04/− 0.83	0.85/1.13	
R^2	0.19/0.25	0.15/0.19	0.35/0.34
Basidiomycota–Canopy–Open	**3.35*****/**2.75****	1.35/2.81**	**7.94*****/**9.83*****
Basidiomycota–Beech–Canopy–Open	− 1.26/− 2.17*	**2.27*/5.17*****	**2.46*/3.34*****
Basidiomycota–Fir–Canopy–Open	**5.57*****/**5.51*****	− 0.04/− 0.27	**8.38*****/**10.10*****
Ascomycota–Canopy–Open	**− 4.62*****/**− 4.80*****	− 1.70/− 1.77	**5.92*****/**6.52*****
Ascomycota–Beech–Canopy–Open	**− 3.67*****/**− 3.48*****	− 0.90/− 0.98	**4.53*****/**5.72*****
Ascomycota–Fir–Canopy–Open	**− 3.36*****/**− 3.68*****	− 1.59/− 1.61	**4.40****/**4.09*****

Table 1. Linear mixed-effects model of the effect of canopy openness on observed community fruit body traits. We first tested the effect of the main predictor, canopy openness, on the full community. We then tested the interaction between lineages and canopy; and between lineages, tree species, and canopy. Effect sizes (z values) are displayed for the linear mixed models with a random effect 'plot in block'. On the left side of each column, the effects of the observed community trait are shown. On the right, the effects for the standardized community trait are based on a null model. Significances are indicated by asterisks, where '*' corresponds to $p < 0.05$, '**' to $p < 0.01$ and '***' to $p < 0.001$. Significant effects were highlighted in bold if both the observed community mean and the standardized effect size (SES) of the community traits were significant. The coefficient of determination is given as marginal R^2.

area across species of different biomes. Evergreen species of the Mediterranean Basin, where frequent drought occurs, have the highest dry leaf mass per unit area, resulting from increased thickness. In experiments, dry leaf mass per unit area was higher under elevated light and temperature but also water stress[47]. Thus hard leaves are adaptations of plants towards heat and drought[44,48]. Although such detailed studies are missing for fungal fruit bodies, we carefully suggest (please see limitations below) that fruit body toughness is an adaptation towards heat, drought, and radiation. We thus suggest the toughness-protection hypothesis for macrofungi, stating an advantage of tough-fleshed fruit bodies in hot and dry environments. Finally, we found a stronger effect size of fruit body toughness than fruit body size and color lightness on the microclimatic scale (Table S3). Previous studies showed the relevancy of fruit body size and color on macroclimatic scales[26,27]. Thus, further studies should test if fruit body toughness explains fungal occurrence on macroecological scales. For example, whether biomes associated with hard-leaved plant species also selects for tough-fleshed fungal fruit bodies, e.g., in the Mediterranean biome[44].

Our results may be carefully interpreted in terms of future climates with more frequent heat and drought periods. Under such conditions, we suggest an increased selection for tough-fleshed fruiting bodies based on our results because they are more likely to be able to endure such conditions. However, whether future climates select for tough-fleshed fruit bodies depends on further considerations. For example, climate change led to a size decline in insect species because maturation is delayed for several reasons, including constrained feeding activities[49]. Similarly, tough-fleshed fruit bodies (e.g., *Fomes* ssp.) require more time to be built up than soft-fleshed fruit bodies (e.g., *Pluteus* ssp.)[50]. Therefore, growth conditions must be suitable over a longer period with more chances of weather extremes interrupting the growth and maturation of the fruit body. Thus tough-fleshed fruit bodies may also be disadvantageous under increasing weather extremes. Therefore, studying fruit body development under harsh conditions from primordium (initial fruit body structure) to maturation (release of spores) of tough- and soft-fleshed species will help understand fungal responses to climate change.

Body size was studied frequently, revealing a body size decline across animals and plants due to climate change[3,49]. Whether fruit body-forming fungi respond with a size decline of mycelium and fruit bodies is unknown. On a global scale, fungal mushrooms communities were smaller in boreal and tropical compared to those in temperate climates[27]. Besides body size, color lightness has been frequently studied in animals and recently also in fungi[26,51]. We expected significant and general responses of fruit body size and color lightness across lineages and hosts, given the prior knowledge based on the existing macroecological studies. We found no consistent community response means of fruit body size and color lightness across lineages or tree species with canopy openness (Fig. 2). However, we found a consistent response of community fruit body size within Ascomycota. Ascomycota communities had smaller fruit bodies under open canopies (Fig. 3, Table 1). Smaller fruit bodies with a higher surface-area to volume ratio get rid of excess heat more rapidly, potentially lowering heat stress under open canopies ('heat-up-cool-down hypothesis'). Although not significant, Ascomycota communities are generally darker than Basidiomycota communities (Fig. 2), and thus, smaller fruit bodies could potentially counteract overheating via darker fruit bodies, which may counteract damage by radiation ('photo-protection hypothesis'). Due to the generally small size of most Ascomycota fruit bodies, their fruit bodies develop more closely to the dead-wood surface, which can reach high temperatures under open canopies (Fig. S1). Thus, a rapid release of excess heat may be beneficial for very dark fruit bodies. We found even smaller

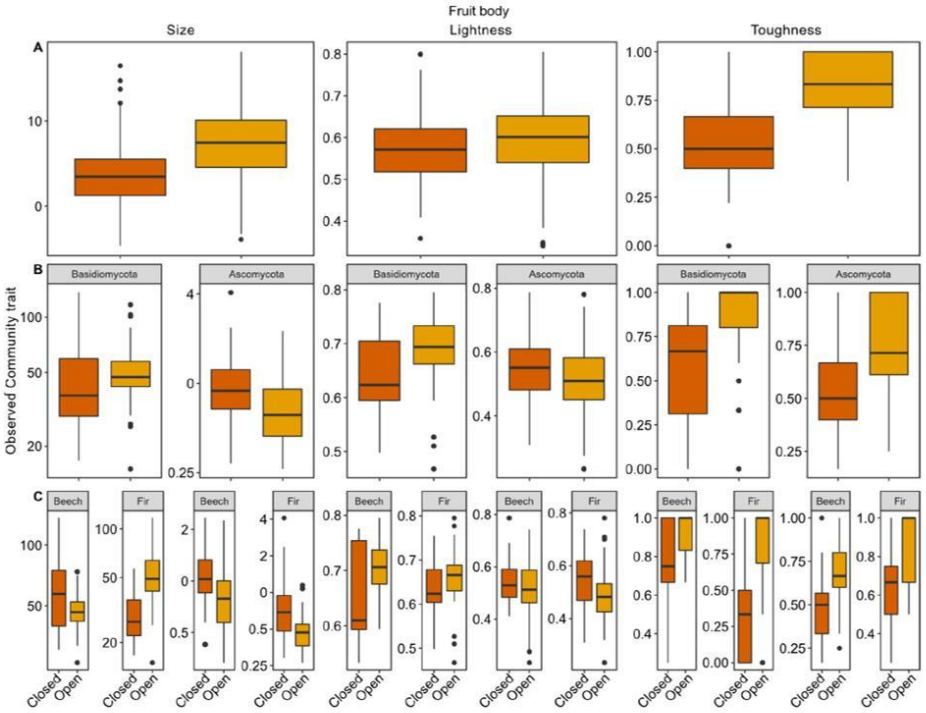

Figure 3. Response of the observed community traits with canopy openness. (**A**) Overall community trait response to canopy openness. Dark orange refers to closed canopies, light orange to open canopies. (**B**) Effects of canopy openness on the community trait separated for Basidio- and Ascomycota. (**C**) Effects of canopy openness on the community trait separated for lineages and tree species. For a statistics table based on a multivariate linear mixed-effects model, see Table 1. Note that fruit body size and color lightness were $\log_{10}$-transformed. The unit of fruit body size is millimetres, the unit of lightness and toughness is percentage. R programming environment version 4.1.2[40] and R add-on package *ggplot2*[41].

fruit bodies under open canopies, which would further support this explanation (Fig. 3). Generally, studies on traits in microclimates are scarce. Studies on ant and spider communities found that warmer temperatures under open canopies correlate with larger body size[52–55]. This finding is in contrast to our findings for Ascomycota. One explanation may be that the fruit bodies of most Ascomycota macrofungi are sessile. Insects and spiders, on the other hand, may move in and out of the sunlight to regulate the thermal body condition and thus benefit from better growth conditions while not being affected by harsh conditions.

Finally, our study also contains limitations. First, our data is limited to understanding the full underlying processes shaping fruiting communities. As pointed out in the introduction, the absence of fruit bodies may have other reasons than a maladaptation of the fruit body, e.g., unfavorable mycelial growth conditions. This may have consequences for our inferences and interpretation. Either the fruiting community may be an artefact of the underlying changes in the mycelium community, or even if mycelium communities do not differ between microclimates, fruiting cues may differ (e.g., enhanced damage of the mycelium in harsh microclimate[22]). Differences in fruiting cues may lead to a different subset of the fruiting community. In both cases, differences in the fruiting community between microclimates would not be related to fruit body traits. The species within the fruiting community may differ, however, the trait distribution between microclimates should not differ from a random draw if they are not associated with the microclimate[56,57]. By applying a null model approach, we demonstrated that the response to microclimate differs from a random draw accounting to some extend for uncertainties (Fig. 4, Table 1). Further studies should therefore consider mycelium in their analyses and ideally perform laboratory experiments where microclimate, fruiting cues, and species traits can be manipulated. Second, mycelium or fruiting community changes may not be related to the microclimate but, e.g., associated changes in biotic interactions. Nevertheless, those fungi that produced mature fruit bodies (recorded in our study) should still possess adaptations that allow them to cope with the harsh microclimate. Further, if biotic interactions lead to the observed pattern, this may result from microclimates if our treatment modifies biotic interactions. Thus laboratory studies are required to disentangle independent effects of heat, drought and biotic

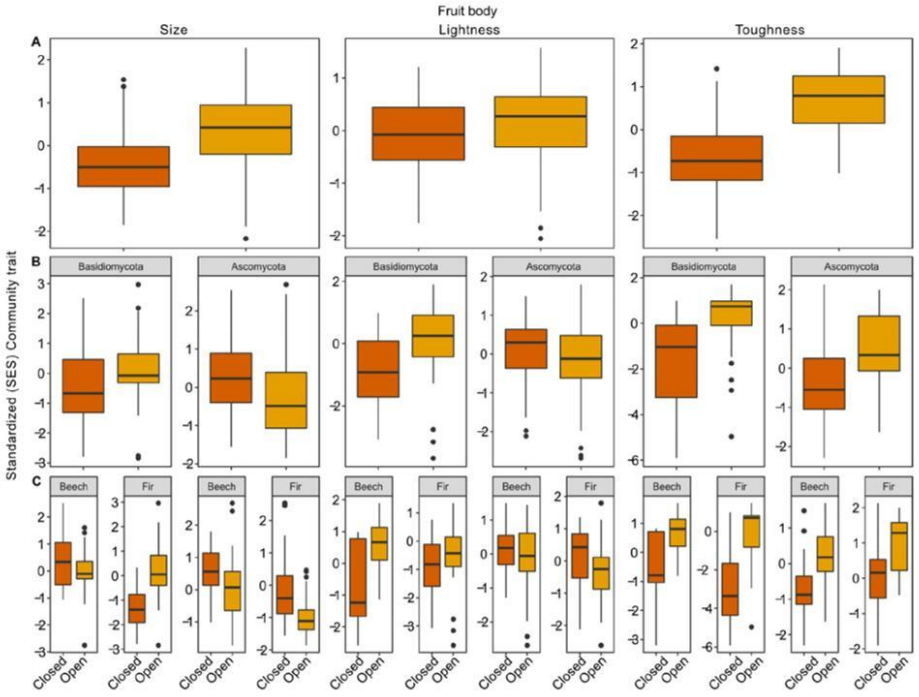

Figure 4. Response of the standardized effect size of the community fruit body traits with canopy openness. Dark orange refers to closed canopies, light orange to open canopies. Standardized effect sizes (SES) were computed based on the independent swap null model. (**A**) Effects of canopy openness on the overall community trait. (**B**) Effects of canopy openness on the community trait separated for Basidio- and Ascomycota. (**C**) Effects of canopy openness on the community trait separated for lineages and tree species. For a statistics table based on a multivariate linear mixed-effects model, see Table 1. R programming environment version 4.1.2[40] and R add-on package *ggplot2*[41].

interactions on fungal mycelium and reproductive growth, e.g., using climate chambers. Third, due to the absence of prior knowledge for most traits in fungal fruit bodies, we restricted our analysis to trait data retrieved from literature (size), photo-measurements (color), and expert knowledge (toughness). The traits were not measured from the specimens which occurred in our study. Thus, the actual traits in situ may differ from those we used. Nonetheless, using average species traits to understand mechanisms of species-environment has considerable value in itself[58]. Ideally, further studies also include intraspecific trait variability[59] to understand how plastic macrofungi can respond to the microclimate. Fourth, our coding of toughness is based on expert knowledge. Expert knowledge has been demonstrated to be a reliable measure of fruit body traits[60]. One option of directly measuring toughness might be the use of penetration measures, e.g., using a penetrometer. This way, a unique quantification method can be used across species and lineages. However, currently, we are not aware of any study that measured fruit body toughness using quantitative methods.

In conclusion, although trait-based studies in fungi are generally increasing, such efforts are still rare in macrofungi. Our study suggests that differences in the fruiting community between microclimates may be related to differences in fruit body morphology. Morphological traits in harsh microclimates may be relevant to secure fungal reproductive success (fructification until spore release). Climate warming induces more frequent weather extremes and microclimatic harshness[5,61]. Our study suggests that harsh microclimates select species with tough-fleshed fruit bodies in Basidio- and Ascomycota. However, to fully understand how microclimate affects macrofungi, future studies should consider mycelium and reproductive growth (maturation) and sporulation and how morphological traits relate to these processes.

Material and methods

Study site and design. This study was part of a larger dead-wood experiment[18] situated in the management zone of the Bavarian Forest National Park in south-eastern Germany characterized by mixed montane forest, consisting of Norway Spruce (*Picea abies* (L.) H. Karst), European Beech (*Fagus sylvatica* L.) and Silver Fir (*Abies alba* Mill.)[62]. For this study, 120 plots of each 0.1 ha were used in a random block design of five blocks. In

autumn 2011, we freshly cut and directly deposited (within less than eight weeks) dead-wood logs (coarse woody debris; mean diameter ± SD = 33 ± 6.5 cm, length = 5 m) of beech and fir. The wood objects were taken from trees of the same age that were harvested from a forest stand of 5 ha of the same elevation. The trees harvested were pairwise, not more distant than 100 m. Further, the soil followed the same homogenous geology (Bohemian Massif, granitic and gneissic bedrock[62]). Each block contained 24 plots, of which half were under open and half under a closed canopy. Further, half of the plots contained a low amount of local dead wood (4 logs of ca. 10 m^3 ha^{-1}), and the other half had a high amount of local dead wood (40 logs of ca. 100 m^3 ha^{-1}). Finally, each block-canopy-amount treatment consisted of two plots with two beech logs, two plots with fir logs, and two plots with one beech and one fir logs. To precisely characterize the amount of dead wood per plot, we calculated the surface area of each object using the formula for a truncated cone. We summed the surface area of all logs and of the sampled objects separately (see below). The surface area was calculated from the length and diameters measured on both ends of each object. To avoid shading by a dense grass layer surrounding the dead-wood logs under open canopies, each plot was mowed once a year during the growing season (for details, see[18]). The open canopies resulted from clearings; an area of 0.1 ha was freed from living or dead trees. Wood surface temperatures were measured on top of 136 logs on a clear summer day, with each five measures per log (half in open, half under closed plots across the four blocks) in August 2018 using an infrared thermal sensor on a summer day[17]. We found differences in temperature between open and closed canopies (Fig. S1).

Fruit body sampling. We sampled fruit bodies on two logs on each plot for four consecutive years (2012–2015) from a total of 320 sampled objects (hosts). The first year was excluded because records were too few to calculate meaningful community trait means (see "Statistical analysis"). The yearly sampling was during late summer and fall (July–October), the main season of fruit body development[63]. All visible fruit bodies were identified in the field or, if necessary, in the laboratory with the aid of a microscope. Voucher specimens were deposited in the herbarium of the Bavarian Forest National Park. The nomenclature followed MycoBank[64]) and a complete species list is available (Table S1). We considered (i) stipitate- and sessile-pileate Basidiomycota and (ii) Ascomycota with Perithecia or Apothecia. We coded the character values "stipitate- pileate" and "sessile-pileate" based on an published coding dataset of fruit body types for 8400 species[30]. Using this dataset, we used only species which were coded either as "stipitate-pileate" or "sessile-pileate". We choose to use stipitate- and sessile-pileate as well as Perithecia or Apothecia, to standardize our dataset to fruit body traits where meaningful size measures are available. Based on the fruit body inventories, we produced a presence/absence community matrix. It was recommended that multiple years and surveys are necessary to gain a robust measure of the community[60], and therefore, we summed occurrences across the sampling years.

Trait data. We extracted the minimum and maximum width of the fruit body from the literature and public websites (http://www.fungi-without-borders.eu, http://www.pilze-ammersee.de/). Based on the minimum and maximum diameter/width derived from these resources, we calculated the mean fruit body size. In the case of pileate-stipitate Basidiomycota and Apothecia of Ascomycota, we used the diameter of the round-shaped cap. In the case of pileate-sessile Basidiomycota and Perithecia of Ascomycota, we used the width of the fruit body (see Fig. 1 for fruit body types).

We further assembled the color lightness of each species, which is the lightness from the HSL (hue, saturation, lightness) color space model[65]. Therefore, we used a publicly available photograph of each species (mycokey.com, mykoweb.com, 123pilze.de, mushroomobserver.org, mushroomexpert.com, etc.) and sampled nine color pixels from the fruit body photograph, following the protocol developed previously[26]. The protocol entails a quality standard of the photographs, e.g., not over- or underexposed by light, and areas on the surface with dirt or leaves should not be sampled. The nine samples were averaged for each species. This protocol is a reliable approach to estimate fruit body color lightness based on the HSL color space model and was shown to be free from geographic bias and was consistent with color lightness derived from standardized fruit body drawings[26].

Finally, we attributed each species to either soft- or tough-fleshed (fruit body toughness). Currently, no framework exists to code fruit body toughness across fruit body types and lineages. We thus choose coding based on expert opinion. Consultation of expert knowledge is a robust approach, which has been used to assemble fruit body traits[60]. Based on expert knowledge (among authors and others, see *Acknowledgements*), we first decided to choose two toughness states and then coded all species accordingly. We decided on binary coding, to reflect extremes of toughness. We thus defined tough-fleshed as either hard as wood (e.g., *Fomes* ssp.) or tough (e.g., *Oligoporus* ssp.) as opposed to soft, which was defined as agaricoid softness (e.g., *Agaricus* ssp.). We coded Polyporales, Gloeophyllales, Hymenochaetales as tough-fleshed, and Agaricales as soft-fleshed. This coding roughly reflects the mitic system with agarics having mainly monomitic hyphal system, whereas most Polyporales, Gloeophyllales, and Hymenochaetales have mostly di-, or trimitic hyphal system[66]. The mitic system is not present in Ascomycota. Based on the coding by the authors, fungi with Perithecia were coded as tough-fleshed as opposed to fungi with Apothecia, which were coded as soft-fleshed. Since Basidio- and Ascomycota differ substantially in fruit body size (see above) and toughness, we analysed the datasets for both lineages separately. Please finally note that we were able to retrieve fruit body size for 106, fruit body lightness for 105 and fruit body toughness for 107 species out of 107 species.18/01/2022 21:08:00.

Statistical analysis. Statistical analyses were conducted in the programming environment R 4.1.2[40] and images were produced with the add-on R package *ggplot2*[41].

Community data and community trait calculation. To test for differences in fungal fruit body traits between closed and open canopies, we calculated the community trait for each dead-wood log community based on the

presence/absence of species. To compute meaningful community traits for each dead-wood log, we used only logs with at least three species. We also considered a threshold of at least one species per log and found consistent results; we further tested a threshold of five species, however, for Basidiomycota on fir, the data was not enough for meaningful estimates. Nonetheless, the overall estimates were consistent with the three species threshold (data not shown).

We computed three response variables. The first response variable was the mean of the $\log_{10}$-transformed mean cap diameter across species of each log[28]. The second response variable was the mean of the $\log_{10}$-transformed cap color lightness across species of each log. The third response variable was the proportion of tough-fleshed fruit bodies on a log, which was computed as the number of tough-fleshed species divided by the total number of species on a log. Before subjecting the community fruit body toughness to the model, it was arc-sin-transformed to reach a Gaussian distribution. We calculated the community traits for three data subsets: overall considering the full community matrix across lineages; and separately for the lineages: for Basidiomycota and for Ascomycota.

Null models. It was previously shown that species richness differs between tree species and canopy openness[18]. Thus, species richness co-varies with the community trait value. Further, the trait pattern observed may also stem from a changed mycelium community, which may have differing fruit body morphology independently of microclimate (artifact scenario). In this case, we would expect a random distribution of traits with microclimate. To account and test for both, an uneven number of species and the artifact scenario, we used a null model ("independent swap") that randomizes species occurrence across sites but fixes both marginal sums for sites (i.e., species richness of sites) and marginal sums for species (i.e., occupancy of logs across the plots). We first calculated the observed community trait for each log. We then randomized the community data matrix 100 times with the independent swap algorithm[56] and calculated for each randomized community matrix the community trait. Finally, we calculated the standardized effect size (SES) by subtracting the expected mean (mean across all randomizations) from the observed mean and dividing the difference by the standard deviation across the randomizations for each plot. For the community null model randomization, we used the function *randomizeMatrix* in the R package picante[67] and used the argument "null.model = 'independentswap' ". A significant response of both the observed and SES community trait indicates non-random pattern of community traits in the microclimates[56,68].

Lineage-based trait differences. We were first interested in the general community trait differences between Basidio- and Ascomycota. Generally, different community traits may explain differences in response with our treatment variable (canopy openness). Thus, we used LMEs with the same random effect as above to test the three community traits against lineage separately while using the other traits as covariates (see below).

Community trait responses with canopy openness. To assess our hypotheses, we tested the effect of canopy openness on community traits. Testing multiple hypotheses based on the same dataset may lead to unreliable significances (random false positive) due to multiple testing[69]. To account for this issue and test the five hypotheses, we followed three approaches: (1) We tested for covariance among the community trait means and the other covariates. Strong collinearity among co-variables in a model can cause spurious effects and distort models. All pairwise correlation coefficients among the trait variables showed correlation coefficients of $|r| < 0.7$, a threshold that was recommended not to exceed[70] to avoid collinearity (Table S2; highest value: 0.66). (2) We fit linear mixed-effects models (LMEs) using the R package *lmer*[71] and tested the effect of canopy openness on each community trait. In each LME model, we also considered the other two community means as covariates to retain the other variables in the model. (3) Finally, we fit a generalized linear model (GLM, binomial family) with canopy openness as the response variable and fruit body size, color lightness and toughness as predictor variables. This model approach allowed us to integrate all community means in one model to avoid multiple testing in separate models.

Effects of canopy openness on the community traits may be mediated or offset by other factors. Thus, we considered the following variables in the LME and GLM modes. (1) Fungal fruiting communities were shown to significantly differ between tree species[18,72]. For this reason, we included tree species as a binary factor in the overall model and, by using interaction terms, estimated all effects also separately for tree species. (2) Further, the amount of dead wood in the direct proximity of a dead-wood object may affect the stand-microclimate, e.g., with high amount of dead wood capturing and maintaining more moisture than plots with a low amount of dead wood. Thus, we included the sum of surfaces of all logs on a plot in the overall and tree models. The total log surface, however, was not significant in any model. Further, in a previous study testing the effect of this effect on species richness and community composition found no significant effect[18]. Thus, we dropped it from the final models. (3) We used dead-wood logs of the same approximate size, however, the variation may still affect species numbers with slightly larger logs having more species[73]. Thus, to standardize the estimates to the same sampling effort, we additionally added the sampled surface to the models. This variable was significant in no model across observed and standardized community traits. We dropped it from the final models. (4) In the LME models, we further included a random effect, which was 'plot in block.'

For the LME, we first fit a model with the main fixed effect canopy openness and tree species as further fixed effect covariates (hereafter "overall model"). Note that in this model, we did not include lineage as an effect because the community traits were calculated for the full community matrix. Then we fit a model with an interaction between lineage (Basidio- and Ascomycota), the tree species (Beech and Fir) and canopy openness (closed and open canopy). The interaction was specified by a "*" in the *lmer* function. To test for the pairwise interactions, we used the function *lsmeans* from the R package lsmeans[74]. Using the *lsmeans* function, we first tested for the interaction between lineage and canopy openness to retrieve an estimate of the community trait

response with canopy, separate for Basidio- and Ascomycota. Second, we tested the interaction between tree species, lineage and canopy openness to retrieve an estimate of the community trait response with canopy, separate for tree species within lineages. In the GLM we tested for the interactions between lineage, tree species and the predictors using the ":" interaction parameter.

Ethical approval. The use of plant parts in present study compiles with international, national and/or institutional guidelines. Voucher specimens were deposited in the herbarium of the Bavarian Forest National Park by Lothar Krieglsteiner, Peter Karasch, Andreas Gminder and Frank Dämmrich.

Data availability

Data and R code are available via DRYAD (https://doi.org/10.5061/dryad.wh70rxwnx).

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Author contributions
F-S.K. and C.B. conceived the concept of the study. C.B., J.M., and R.B. designed the experimental setting of the study. F-S.K. analyzed the data and wrote the first draft of the manuscript. C.B. contributed to data analysis, interpretation and writing of the manuscript. J.S. contributed to writing of the manuscript. All authors critically revised the manuscript.

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Fungal fruit body assemblages are tougher in harsh microclimates

Supplementary Material

Supplementary Tables

Table S1 Species list of the species found in this study with values for the fruit body traits.

Phyllum	Species	Fruit body width (mm)	Fruit body lightness	Fruit body toughness	Fruit body type
Ascomycota	*Ascocoryne cylichnium*	12.50	0.69	soft-fleshed	Apotecium
Ascomycota	*Ascocoryne sarcoides*	7.50	0.64	soft-fleshed	Apotecium
Ascomycota	*Ascocoryne solitaria*	17.50	0.46	soft-fleshed	Apotecium
Ascomycota	*Barbatosphaeria barbirostris*	0.40	0.57	tough-fleshed	Peritecium
Ascomycota	*Bertia moriformis*	0.75	0.62	tough-fleshed	Peritecium
Ascomycota	*Bisporella citrina*	2.00	0.48	soft-fleshed	Apotecium
Ascomycota	*Bisporella pallescens*	1.25	0.38	soft-fleshed	Apotecium
Ascomycota	*Calycina discreta*	0.80	0.90	soft-fleshed	Apotecium
Ascomycota	*Calycina languida*	0.35	0.89	soft-fleshed	Apotecium
Ascomycota	*Chaetosphaeria myriocarpa*	0.15	0.49	tough-fleshed	Peritecium
Ascomycota	*Zignoella ovoidea*	0.15	0.19	tough-fleshed	Peritecium
Ascomycota	*Claussenomyces atrovirens*	0.40	0.22	soft-fleshed	Apotecium
Ascomycota	*Coniochaeta ligniaria*	0.50	0.10	tough-fleshed	Peritecium
Ascomycota	*Coniochaeta malacotricha*	0.50	0.48	tough-fleshed	Peritecium
Ascomycota	*Coniochaeta pulveracea*	0.50	0.81	tough-fleshed	Peritecium
Ascomycota	*Coniochaeta subcorticalis*	0.50	NA	tough-fleshed	Peritecium
Ascomycota	*Coniochaeta velutina*	0.50	0.53	tough-fleshed	Peritecium
Ascomycota	*Cosmospora coccinea*	0.30	0.73	tough-fleshed	Peritecium
Ascomycota	*Hypocrea gelatinosa*	2.00	0.80	soft-fleshed	Apotecium
Ascomycota	*Cyathicula cyathoidea*	1.50	0.55	soft-fleshed	Apotecium
Ascomycota	*Exarmidium inclusum*	0.15	0.23	tough-fleshed	Peritecium
Ascomycota	*Haglundia perelegans*	2.00	0.51	soft-fleshed	Apotecium
Ascomycota	*Hamatocanthoscypha laricionis*	0.25	0.42	soft-fleshed	Apotecium
Ascomycota	*Helminthosphaeria stuppea*	0.65	0.18	tough-fleshed	Peritecium
Ascomycota	*Hyaloscypha aureliella*	0.35	0.67	soft-fleshed	Apotecium
Ascomycota	*Hymenoscyphus scutula*	2.75	0.55	soft-fleshed	Apotecium
Ascomycota	*Hymenoscyphus virgultorum*	2.75	0.60	soft-fleshed	Apotecium
Ascomycota	*Lachnellula calyciformis*	2.50	0.83	soft-fleshed	Apotecium
Ascomycota	*Lachnum virgineum*	0.75	0.51	soft-fleshed	Apotecium
Ascomycota	*Lasiosphaeria canescens*	3.00	0.26	tough-fleshed	Peritecium
Ascomycota	*Lasiosphaeria hirsuta*	3.00	0.21	tough-fleshed	Peritecium
Ascomycota	*Lasiosphaeria ovina*	3.00	0.89	tough-fleshed	Peritecium
Ascomycota	*Lasiosphaeria spermoides*	3.00	0.23	tough-fleshed	Peritecium
Ascomycota	*Lasiosphaeria strigosa*	3.00	0.40	tough-fleshed	Peritecium
Ascomycota	*Lophiotrema boreale*	0.70	0.58	tough-fleshed	Peritecium
Ascomycota	*Lophium mytilinum*	0.65	0.84	tough-fleshed	Peritecium
Ascomycota	*Melanomma sanguinarium*	0.40	0.40	tough-fleshed	Peritecium
Ascomycota	*Mollisia aquosa*	0.60	0.91	soft-fleshed	Apotecium
Ascomycota	*Mollisia fusca*	1.10	0.76	soft-fleshed	Apotecium
Ascomycota	*Mollisia ligni*	1.25	0.63	soft-fleshed	Apotecium
Ascomycota	*Mollisia olivaceocinerea*	0.65	0.49	soft-fleshed	Apotecium
Ascomycota	*Natantiella ligneola*	0.40	0.76	tough-fleshed	Peritecium
Ascomycota	*Nectria cinnabarina*	0.25	0.61	tough-fleshed	Peritecium
Ascomycota	*Nectria coccinea*	0.25	0.61	tough-fleshed	Peritecium
Ascomycota	*Dialonectria episphaeria*	0.25	0.50	tough-fleshed	Peritecium

Ascomycota	*Nectria fuckeliana*	0.25	0.46	tough-fleshed	Peritecium
Ascomycota	*Nectria magnusiana*	0.30	0.59	tough-fleshed	Peritecium
Ascomycota	*Nectria peziza*	0.30	0.47	tough-fleshed	Peritecium
Ascomycota	*Ombrophila janthina*	2.50	0.28	soft-fleshed	Apotecium
Ascomycota	*Orbilia coccinella*	0.18	0.65	soft-fleshed	Apotecium
Ascomycota	*Orbilia delicatula*	0.75	0.30	soft-fleshed	Apotecium
Ascomycota	*Patinella sanguineoatra*	1.00	0.22	tough-fleshed	Apotecium
Ascomycota	*Pezicula acericola*	1.25	0.28	soft-fleshed	Apotecium
Ascomycota	*Pezicula cinnamomea*	0.45	0.67	soft-fleshed	Apotecium
Ascomycota	*Phaeohelotium carneum*	0.65	0.26	soft-fleshed	Apotecium
Ascomycota	*Phaeohelotium trabinellum*	0.60	0.28	soft-fleshed	Apotecium
Ascomycota	*Polydesmia pruinosa*	0.50	0.49	soft-fleshed	Apotecium
Ascomycota	*Rosellinia aquila*	1.25	0.74	tough-fleshed	Peritecium
Ascomycota	*Rosellinia thelena*	1.25	0.89	tough-fleshed	Peritecium
Ascomycota	*Scutellinia cejpii*	4.50	0.66	soft-fleshed	Apotecium
Ascomycota	*Scutellinia scutellata*	4.50	0.59	soft-fleshed	Apotecium
Ascomycota	*Scutellinia subhirtella*	5.00	0.63	soft-fleshed	Apotecium
Ascomycota	*Symbiotaphrina microtheca*	0.40	0.75	tough-fleshed	Apotecium
Ascomycota	*Tympanis hypopodia*	0.75	NA	soft-fleshed	Apotecium
Ascomycota	*Tympanis truncatula*	0.75	0.73	soft-fleshed	Apotecium
Basidiomycota	*Bjerkandera adusta*	55.00	0.84	tough-fleshed	pileate-sessile
Basidiomycota	*Clitocybe ditopa*	27.50	0.53	soft-fleshed	pileate-stipitate
Basidiomycota	*Clitopilus hobsonii*	8.50	0.70	soft-fleshed	pileate-stipitate
Basidiomycota	*Coprinus domesticus*	25.00	0.58	soft-fleshed	pileate-stipitate
Basidiomycota	*Coprinellus micaceus*	19.00	0.61	soft-fleshed	pileate-stipitate
Basidiomycota	*Crepidotus cesatii*	18.00	0.39	soft-fleshed	pileate-sessile
Basidiomycota	*Crepidotus pallidus*	1.20	0.65	soft-fleshed	pileate-sessile
Basidiomycota	*Flammulaster carpophilus*	10.00	0.65	soft-fleshed	pileate-stipitate
Basidiomycota	*Gloeophyllum sepiarium*	72.50	0.50	tough-fleshed	pileate-sessile
Basidiomycota	*Gymnopilus sapineus*	42.50	0.56	soft-fleshed	pileate-stipitate
Basidiomycota	*Hohenbuehelia atrocoerulea*	20.00	0.34	soft-fleshed	pileate-sessile
Basidiomycota	*Hohenbuehelia fluxilis*	11.00	0.29	soft-fleshed	pileate-sessile
Basidiomycota	*Hohenbuehelia pinacearum*	7.00	0.39	soft-fleshed	pileate-sessile
Basidiomycota	*Hypholoma capnoides*	40.00	0.56	soft-fleshed	pileate-stipitate
Basidiomycota	*Hypholoma fasciculare*	40.00	0.66	soft-fleshed	pileate-stipitate
Basidiomycota	*Hypholoma marginatum*	30.00	0.48	soft-fleshed	pileate-stipitate
Basidiomycota	*Inonotus hastifer*	NA	0.62	tough-fleshed	pileate-sessile
Basidiomycota	*Inonotus nodulosus*	105.00	0.73	tough-fleshed	pileate-sessile
Basidiomycota	*Irpex lacteus*	400.00	0.73	tough-fleshed	pileate-sessile
Basidiomycota	*Ischnoderma benzoinum*	55.00	0.64	tough-fleshed	pileate-sessile
Basidiomycota	*Laxitextum bicolor*	90.00	0.36	tough-fleshed	pileate-sessile
Basidiomycota	*Mycena amicta*	11.50	0.67	soft-fleshed	pileate-stipitate
Basidiomycota	*Mycena galopus*	15.00	0.65	soft-fleshed	pileate-stipitate
Basidiomycota	*Oudemansiella mucida*	60.00	0.57	soft-fleshed	pileate-stipitate
Basidiomycota	*Panellus mitis*	17.50	0.65	soft-fleshed	pileate-sessile
Basidiomycota	*Panellus serotinus*	65.00	0.63	soft-fleshed	pileate-sessile
Basidiomycota	*Panellus stypticus*	27.50	0.75	soft-fleshed	pileate-sessile
Basidiomycota	*Panellus violaceofulvus*	16.50	0.57	soft-fleshed	pileate-sessile
Basidiomycota	*Pholiota cerifera*	75.00	0.80	soft-fleshed	pileate-stipitate
Basidiomycota	*Pholiota lenta*	75.00	0.75	soft-fleshed	pileate-stipitate
Basidiomycota	*Pholiota tuberculosa*	35.00	0.52	soft-fleshed	pileate-stipitate
Basidiomycota	*Pluteus semibulbosus*	35.00	0.56	soft-fleshed	pileate-stipitate
Basidiomycota	*Polyporus brumalis*	35.00	0.75	tough-fleshed	pileate-stipitate
Basidiomycota	*Postia caesia*	40.00	0.35	tough-fleshed	pileate-sessile
Basidiomycota	*Postia tephroleuca*	35.00	0.48	tough-fleshed	pileate-sessile
Basidiomycota	*Trametes cinnabarina*	65.00	0.59	tough-fleshed	pileate-sessile
Basidiomycota	*Schizophyllum commune*	20.00	0.78	tough-fleshed	pileate-sessile
Basidiomycota	*Simocybe centunculus*	12.50	0.74	soft-fleshed	pileate-stipitate
Basidiomycota	*Trametes gibbosa*	85.00	0.75	tough-fleshed	pileate-sessile
Basidiomycota	*Trametes hirsuta*	57.50	0.76	tough-fleshed	pileate-sessile
Basidiomycota	*Trametes versicolor*	60.00	0.71	tough-fleshed	pileate-sessile
Basidiomycota	*Trichaptum abietinum*	20.00	0.71	tough-fleshed	pileate-sessile

Table S2 Pearson correlation coefficient for the observed community mean of three fruit body traits.

		Fruit body size	Fruit body lightness	Fruit body toughness	Plot surface (all logs)
Overall	Fruit body size	–	0.38	0.25	0.05
	Fruit body lightness	0.38	–	0.08	-0.06
	Fruit body toughness	0.25	0.08	–	-0.12
	Plot surface (all logs)	0.05	-0.06	-0.12	–
Basidiomycota	Fruit body size	–	0.18	0.54	0.06
	Fruit body lightness	0.18	–	0.45	0.07
	Fruit body toughness	0.54	0.45	–	-0.03
	Plot surface (all logs)	0.06	0.07	-0.03	–
Ascomycota	Fruit body size	–	0.29	-0.66	0.11
	Fruit body lightness	0.29	–	-0.28	-0.04
	Fruit body toughness	-0.66	-0.28	–	-0.06
	Plot surface (all logs)	0.11	-0.04	-0.06	–

Table S3 Generalized linear model (GLM) with canopy as response variable and the three community traits as predictors, allowing to test the hypotheses family in one model. Residuals were modeled with the binomial family because canopy openness is a binary variable. Significant effects are highlighted in bold. Positive z values correlate with higher community values in the open canopy. Groups were tested using interaction terms with ":" in the GLM.

Group		Predictor	Estimate	Std. Error	z value	Pr(>|z|)
Overall		Intercept	-5.45	1.02	**-5.37**	**<0.000**
		Size	2.51	0.48	**5.23**	**<0.000**
		Lightness	-1.24	3.03	-0.41	0.683
		Toughness	4.84	0.63	**7.65**	**<0.000**
Basidiomycota		Size	0.91	0.86	1.06	0.287
Ascomycota		Size	-0.66	0.90	-0.74	0.460
Basidiomycota		Lightness	2.65	5.22	0.51	0.612
Ascomycota		Lightness	-1.75	1.84	-0.95	0.342
Basidiomycota		Toughness	2.23	0.62	**3.62**	**<0.000**
Ascomycota		Toughness	1.91	0.50	**3.84**	**<0.000**
Basidiomycota	Beech	Size	2.63	1.31	**2.01**	**0.045**
Ascomycota	Beech		-1.48	1.43	-1.04	0.298
Basidiomycota	Fir		0.57	1.20	0.48	0.633
Ascomycota	Fir		-2.94	1.64	-1.80	0.072
Basidiomycota	Beech	Lightness	12.83	8.68	1.48	0.139
Ascomycota	Beech		-1.02	2.49	-0.41	0.682
Basidiomycota	Fir		-3.76	7.05	-0.53	0.593
Ascomycota	Fir		-1.39	2.33	-0.60	0.552
Basidiomycota	Beech	Toughness	1.78	0.89	**2.01**	**0.045**
Ascomycota	Beech		4.54	1.03	**4.42**	**<0.000**
Basidiomycota	Fir		3.16	1.12	**2.81**	**0.005**
Ascomycota	Fir		1.58	0.60	**2.61**	**0.009**

Supplementary Figures

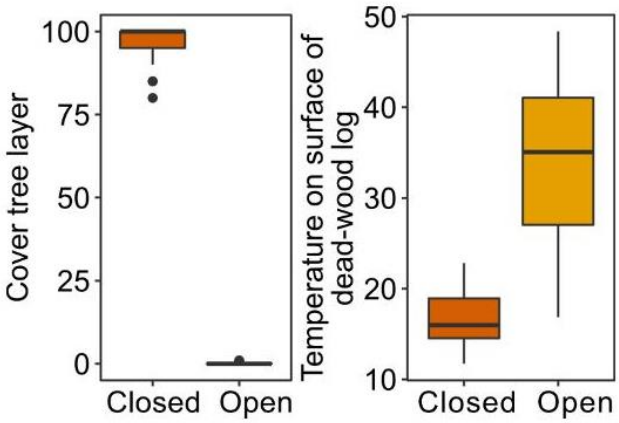

Figure S1 Demonstration of the microclimatic differences between closed (orange) and open canopies (yellow). a) Observational cover of the tree layer. b) Temperature measured on the surface of dead-wood logs on the same sunny day on a subset of the logs in the experiment (5 measures per log. 30 logs in open and 30 logs in closed stand).

10.4 Unraveling the effect of environment and decomposer diversity on deadwood decomposition: Lessons from a large-scale experiment

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Unraveling the effect of environment and decomposer diversity on deadwood decomposition: lessons from a large-scale experiment

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Abstract

Background The decomposition of organic matter is among the most important ecosystem processes in forest ecosystems, regulating the carbon and nutrient cycle. However, our understanding about how direct (environment and decomposer diversity) and indirect effects (environment via decomposer diversity) contribute to deadwood decomposition is limited. We set up a large real-world deadwood experiment in a mixed mountain forest in south-eastern Germany considering beech (*Fagus sylvatica*) and fir (*Abies alba*) as substrates. We simultaneously tested effects of canopy cover, amount and heterogeneity of surrounding deadwood and a broad set of fungal diversity measures mediated by environment on deadwood density loss after 10 years.

Results Deadwood density loss was mainly explained by tree species and canopy cover. Beech showed higher density loss than fir and density loss was larger in open compared to closed canopies. Even though fungal diversity is mediated by environment, the direct effects on density loss were weak and inconsistent across tree species and fungal diversity measures.

Conclusions We found weak support for the fungal diversity–ecosystem process relationship for deadwood decomposition. We suggest that deadwood decomposition and the resulting carbon and nutrient cycles in forest ecosystems are primarily regulated by the tree species selected through forest management and canopy disturbances, particularly in the context of climate change.

Keywords Forest ecosystem, Decomposition, Climate change, Tree species, Forest microclimate, Fungal diversity, Hill series, Structural equation model

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Background

The decomposition of organic matter is among the most important ecosystem processes in forest ecosystems (Benbow et al. 2019), playing a vital role in regulating carbon storage. Deadwood alone stores about 8% of global forest carbon stocks (Pan et al. 2011). In addition, deadwood serves as a habitat for tremendously diverse organisms from the animal, plant, fungi and bacterial kingdoms and thus helps to maintain forest biodiversity (Stokland et al. 2012). Additionally, deadwood is essential for water and nutrient storage as well as soil development (Forrester et al. 2012). However, deadwood decomposition remains one of the least understood part of the forest carbon cycle (Perreault et al. 2023).

Factors affecting deadwood decomposition are complex and depend on the spatial and temporal scale. At global and regional scales, climate has been suggested as the main driver of decomposition rates (e.g., Berg et al. 1993; Currie et al. 2010). However, it has been shown that models can be misleading if the variation of local-scale factors is ignored in such models (Bradford et al. 2014). Therefore, to increase predictability in times of global change, we need to disentangle the complex hierarchical interplay of stand-scale factors (e.g., climate) and object-related factors (e.g., decomposer communities) affecting deadwood decomposition rates.

At stand scale, forest structural variables might directly or indirectly (via change in decomposer communities) affect the decomposition rate of a deadwood object. Variability in canopy cover strongly affects microclimate conditions in forest ecosystems (Zellweger et al. 2020). Canopy openings increase forest floor exposure to sunlight, leading to shifts in temperature and humidity, and greater climate variability, including more extreme microclimates compared to closed canopies (De Frenne et al. 2019). As a result, deadwood is exposed to physical forces linked to these changes. The few existing studies suggest that canopy cover significantly impacts decomposition rates, with higher rates under open compared to closed canopies (Janisch et al. 2005; Shorohova and Kapitsa 2014). The assumed mechanism might be increased solar radiation in open canopies that can enhance photodegradation and thus cause a direct disintegration of the wood (George et al. 2005; Li et al. 2016). Further, under extreme and variable temperature and moisture conditions in open canopies, deadwood might be subject to physical stress (e.g., via cracks) or leaching and weathering causing direct disintegration (Fravolini et al. 2018; Harmon et al. 1986; Russell et al. 2015; Zhou et al. 2007). Indirectly, canopy cover can modify the community of wood-decomposing organisms (Brabcová et al. 2022; Krah et al. 2018; Seibold et al. 2016), thereby affecting decomposition rates via metabolism of environmentally adapted species (Jacobs and Work 2012). At stand scale, the amount of surrounding deadwood may also affect decomposition rates of deadwood directly via modified microclimate conditions. Indeed, a recent study revealed that deadwood temperature is lower in summer if the amount of deadwood in the surrounding is higher suggesting buffering effects (Schreiber et al. 2025). However, deadwood heterogeneity and amount might more indirectly affect the decomposition of an object via mediating the diversity pattern of decomposer communities (i.e., deadwood heterogeneity and amount in the surrounding may positively influence the diversity of saproxylic organisms on individual deadwood objects (Blaser et al. 2013; Seibold et al. 2016). Thus, increasing structural diversity and increasing amount of surrounding deadwood may affect decomposition rates via decomposer diversity.

At object scale, deadwood decomposition is affected by tree species identity, related wood characteristics and wood-decomposing organisms (Austin et al. 2016; Erdenebileg et al. 2020; Jacobs and Work 2012; Shorohova and Kapitsa 2014). Studies have shown that angiosperm wood typically decomposes more rapidly than gymnosperm wood (Herrmann et al. 2015; Kipping et al. 2022; Weedon et al. 2009). This variation in decomposition rates can be attributed to differences in wood traits, which are determined by the chemical and morphological composition of the wood specific to each tree species (Kahl et al. 2017). Traits such as higher nitrogen and phosphorus content, which are more common in angiosperms, enhance decomposition, while traits such as lignin and phenols, more prevalent in gymnosperms, tend to inhibit it (Kahl et al. 2017; Weedon et al. 2009). The impact of these wood traits is most pronounced during the initial stages of decomposition, gradually diminishing over time (Oberle et al. 2020). However, the relative importance of tree species versus other environmental factors on deadwood density loss is, to our knowledge, unknown.

Within an object, deadwood organisms directly break down organic matter for resource exploitation. In temperate and boreal forests, wood-decaying fungi are the most efficient organisms of deadwood decomposition (Gómez-Brandón et al. 2020; Perreault et al. 2023). Fungi utilize a broad range of extracellular enzymes (e.g., ligninolytic enzymes; Arnstadt et al. 2016) and use other non-enzymatic strategies (e.g., hydroxyl radicals) to degrade all components of wood (Goodell et al. 2017). However, the relationship between the diversity of wood-decaying fungi and decomposition is not straightforward. For example, studies showed positive (e.g., Kahl et al. 2015; Lustenhouwer et al. 2020) and negative (e.g., Fukasawa and Matsukura

2021; Perreault et al. 2023) effects between number of fungal species and decomposition rates, respectively indicating facilitative (e.g., niche complementarity) and antagonistic relationships (such as, e.g., competitive interactions). However, recent studies indicated that the community composition might be a better predictor for decomposition than number of species (Hoppe et al. 2016; Pietsch et al. 2019; Yang et al. 2024). Further, it has been suggested that the prevalence of specific dominant species better explains decay than diversity measures in which all species are treated equally (Kipping et al. 2024). Therefore, more advanced diversity measures in which species within a community will be weighted by their abundance (e.g., Hill numbers) might increase our mechanistic understanding on the diversity–decomposition relationship (Chao et al. 2016). Finally, in a recent study it has been emphasized that inconsistencies in the fungal diversity–decomposition relationship among real-world studies might be caused by an ignorance of environmental factors that affect deadwood decomposition directly and indirectly via diversity (Runnel et al. 2025).

Here, we used a large real-world deadwood experiment to disentangle stand-scale (canopy cover, amount of surrounding deadwood, and heterogeneity of surrounding deadwood) and object-scale (tree species that is, beech and fir, wood-decaying fungal diversity) factors and on the decomposition rate of coarse woody debris after 10 years of succession (Fig. 1). First, we tested direct effects of the environment (stand-scale factors, tree species) and fungal diversity as well as indirect effects of environment via fungal diversity. Second, we tested direct and indirect effects for each tree species separately. To increase inferences, we used fungal alpha- and beta-diversity based on metabarcoding and fruit body inventories and applied the Hill framework to test diversity effects when emphasizing rare, common and dominant species.

Materials and methods

Study area and study design

The long-term dead wood experiment was carried out in the management zone of the Bavarian Forest National Park in southeastern Germany (48°54′N, 13°29′E). The management zone is characterized by a mixed mountain forest with Norway Spruce (*Picea abies* (L.) H. Karst), European Beech (*Fagus sylvatica* L.) and Silver Fir (*Abies alba* Mill.) (Bässler et al. 2011). Mean annual temperature in this zone is ca. 7 °C and mean sum of precipitation ca. 1300 mm (Bässler et al. 2010).

Thirty-six plots, each with a standardized size of 0.1 ha, were established in four different sites (blocks) across the study area (ca. 48 km^2, minimum distance between sites: 2.4 km), with half under closed and half under open canopies (Fig. 1). To create a gradient in the heterogeneity of deadwood, combinations of different tree species and levels of heterogeneity were implemented. The lowest level of heterogeneity includes only one of the four substrate types (fir branches, fir logs, beech branches, or beech logs). The intermediate level of heterogeneity includes either one tree species with both diameter classes (fir logs and fir branches or beech logs and beech branches) or both tree species with one diameter class (fir and beech logs or fir and beech branches). The highest level includes a combination of both tree species and both diameter classes (Fig. 1). The index of deadwood heterogeneity was calculated based on the different substrate types per plot as described by Siitonen et al. (2000) and applied in several studies (e.g., Seibold et al. 2016). The plots contain an overall high amount of branches (mean diameter: 4 cm) and logs (mean diameter: 37.5 cm) (on average: 165.87 m^3) (Fig. 1). However, variability in deadwood amount is considerable and range from 103.37 m^3 to 231.35 m^3 (Fig. S1). Even though deadwood amount is not fully standardized across our study plots, we used it as a predictor. Deadwood amount as a predictor is not skewed across our study plots and uncorrelated with the other predictors (Table S1 and Fig. S1).

Sampling of log disks and fungal data

Log disk sampling and density loss measuring

On each plot, we selected randomly one log, either beech or fir. On six plots, we selected two logs (one beech and one fir), which resulted in a total of 42 logs across all plots. In summary, we analyzed 21 logs in open canopies (11 beech logs, 10 fir logs) and 21 logs in closed canopies (10 beech logs, 11 fir logs) (Table S1). On each log the first 10 cm of the 5-m logs were cut off on one side with a chainsaw. Afterward, a clean log disk with a thickness of about 5 cm was cut off. In the laboratory, the log disks were dried in a drying oven (Memmert U40) at 65 °C until constant weight. Density loss calculation was based on a standardized subsample of each disk. For this purpose, each log disk was divided into four sectors. Within each sector, cylindrical samples were extracted using a hole saw drill (diameter: 40 mm). The number of samples per sector depended on the heterogeneity in decay and disk diameter to ensure representative sampling of each sector's decay characteristics. In most cases, this approach yielded two subsamples per sector, resulting in a total of eight samples per disk for the majority of disks. In a few cases where drilling was not feasible due to advanced wood disintegration, subsamples were obtained using a knife. A test wise increase in the number of

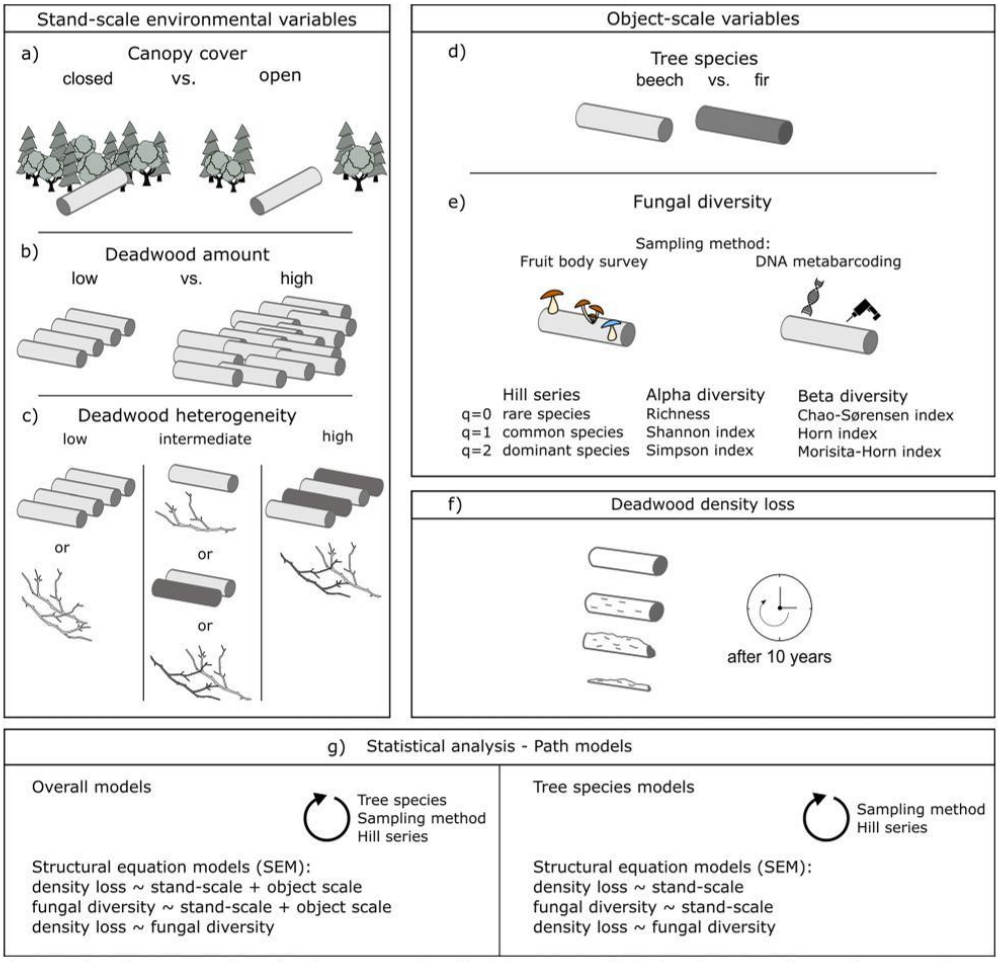

Fig. 1 Deadwood experiment with stand-scale environmental variables (**a**) canopy cover, (**b**) deadwood amount in the immediate surrounding (within the plot), and (**c**) deadwood heterogeneity in the immediate surrounding (within the plot). Levels of heterogeneity (see Materials and methods section for more details) are based on tree species (beech and fir) and deadwood size (logs and branches). In the overall models both object-scale variables were included (**d**) tree species, (**e**) wood-decaying fungal diversity. Fungal diversity was both predictor and response variable in the path models, see Materials and methods section). (**f**) Deadwood density loss is the main response variable in the 12 structural equation models (SEMs). (**g**) SEM path models were divided into overall models, which were performed for each combination of tree species, sampling method, and Hill number (*q*0, *q*1, and *q*2) and into tree species models performed for each combination of sampling method and Hill number (*q*0, *q*1, and *q*2)

subsamples did not alter the density loss estimates derived from this procedure. Each sub-sample was weighed to determine the dry-weight. Then each sub-sample was wrapped airtight with a standardized amount (8 cm^2) of Parafilm®. The volume of each sub-sample was measured using the volume displacement method. A 250 ml measuring cylinder was filled with 150 ml of distilled water, and each Parafilm-treated sub-sample was submerged at a standardized depth by gently pressing it completely underwater with a small wooden stick. The new water level in the cylinder was then recorded. The new fill level was subtracted from

the 150 ml to obtain the volume of the sub-sample. To obtain the density of each sub-sample, the dry weight of the sub-samples was divided by the volume of the sub-sample ($\rho = m/V$). For each log disk, the average density of the log sub-samples was calculated. The percentage of density loss for each log disk was determined using the following formula:

$$densityloss = 100 - \frac{\overline{\rho}}{t_0 density} \times 100, \quad (1)$$

where '$\overline{\rho}$' represents the average density of the individual log disks and 't_0 density' refers to the dry density of freshly cut beech or fir logs as reported by Lohmann (1987). For beech samples, a literature value of 0.68 g/ml was used, and for fir samples, a literature value of 0.41 g/ml was used. Finally, the density loss was calculated for each log disk (Table S1).

Sampling of fungal fruit bodies and fungal DNA for metabarcoding

Fungal fruit body inventories (2012, 2013, 2015, 2018, 2021) were based on fruit bodies that were visible with the naked eye on deadwood objects every autumn (September/October), during the main season of fruit body development in the study area (Halme and Kotiaho 2012; Krah et al. 2018; Schreiber et al. 2024). To ensure an effective and non-redundant sampling, we divided logs into seven segments, two representing the cut edges of the log and five representing the log surface (each 1 m long). Fruit bodies were identified to species level in the field or, if necessary, in the laboratory with the aid of a microscope by mycological professionals (see Acknowledgements). Voucher specimens were deposited in the herbarium of the Bavarian Forest National Park. The complete species list is published and can be found in Schreiber et al. (2024).

Deadwood intended for next-generation sequencing analysis of the fungal community was sampled using a cordless drill (Makita BDF 451), during the same years as the fruit body inventory (2012, 2013, 2015, 2018, 2021). Each selected deadwood object was drilled in four sectors covering in regular distance the whole log, avoiding the very ends of logs. The bark at the drilling point was removed ensuring no mosses, lichens or external spores remain on the bark. A sterilized auger was then driven horizontally into each sector and the dust from all drilling points of each log was combined into one composite sample into sterile plastic bag, stored in presence of cooling blocks over the transport and frozen within a few hours after drilling. The drilled materials were weighed in the laboratory and freeze-dried to estimate the deadwood dry mass. Next, it was milled using an Ultra Centrifugal Mill ZM 200 (Retsch, Germany), and the resulting fine powder was stored in −20 °C and used for the subsequent analyses. Total genomic DNA was extracted from 200 mg of freeze-dried, milled material using the NucleoSpin Soil Kit (Macherey–Nagel, Germany) following to the manufacturer's instructions (see details Baldrian et al. 2016; Brabcová et al. 2022). The fungal community was determined by amplicon sequencing targeting fungal ITS2 region. The ITS2 region was PCR-amplified using barcoded gITS7 and ITS4 primers (Ihrmark et al. 2012) in triplicate PCRs per sample (Baldrian et al. 2016; Brabcová et al. 2022). PCRs contained 5 µl of 5×Q5 reaction buffer, 1.5 µl of BSA (10 mg ml^{-1}), 1 µl of each primer (0.01 mM), 0.5 µl of PCR Nucleotide Mix (10 mM each), 0.25 µl of Q5 High Fidelity DNA polymerase (2 U μl^{-1}, New England Biolabs, Inc.), 5 µl of 5×Q5 HighGC Enhancer and 1 µl of template DNA (approx. 50 ng μl^{-1}). Cycling conditions were 94 °C for 5 min, 35 cycles of 94 °C for 1 min, 62 °C for 1 min, and 72 °C for 1 min, and a final extension at 72 °C for 10 min. PCR triplicate reaction products were pooled and purified (MinElute PCR Purification Kit, Quiagen), and amplicon libraries prepared with the TruSeq DNA PCR-Free Kit LP (Illumina) were sequenced in house on the Illumina MiSeq (2×250-base reads).

The amplicon sequencing data were processed using the SEED 2.1.1 pipeline (Větrovský et al. 2019). In brief, paired-end reads were merged using fastq-join (Aronesty 2013), and the ITS2 region was extracted using ITS Extractor 1.0.11 (Bengtsson-Palme et al. 2013) before processing. Chimeric sequences were identified and removed using Usearch 11.0.667 (Edgar 2010), and sequence clustering was performed using UPARSE implemented within Usearch (Edgar 2013) at 97% similarity. The most abundant sequences from each cluster were matched to species-level taxonomy using BLASTn against UNITE 9 (Nilsson et al. 2019). If the best hit showed less similarity than 97% similarity with 95% coverage, the best genus-level hit was identified. Species-level analyses were conducted by combining operational taxonomic units (OTUs) of the same species and grouping remaining OTUs under the genus of the best hit and labeling them as "sp.". Sequences identified as *Fagus* sp. or *Abies* sp., or non-fungal sequences were excluded. To assign putative ecological functions to the fungal OTUs, the fungal genera of the best hit were classified into ecological categories (e.g., white rot, brown rot, saprotroph, plant pathogen, ectomycorrhiza) based on Põlme et al. (2020). Fungal OTUs not assigned to a genus with known ecophysiology and those assigned to genera with unclear ecology remained unclassified. In the following, the term "species" is used, next to species which were identified by fruit body inventory, for fungal

OTUs, although we are aware that OTUs are only putative species.

Data preparation and statistical analysis

All data preparation and analysis were performed in R 4.1.0 (R Core Team 2021). Our analyses were based on community matrices derived from fruit body sampling and metabarcoding for each year. Abundance of the fruit body community matrices was calculated as the sum of log segments occupied by a species, while for the metabarcoding data, abundance was determined using the number of reads. For the latter, only samples (objects in a given year) with a threshold of total OTU count of more than 1000 reads were included in the analysis. We decided to analyze our data on yearly basis. It is well known that fungal communities change over the course of succession (Frankland 1998; Fukami et al. 2010; Lepinay et al. 2021; Schreiber et al. 2024). Thus, effects of fungal diversity on density loss might vary substantially among years. For example, effects could change systematically across succession or communities at certain successional stage could be key to explain overall density loss. Therefore, biological effects could be masked when analyzing the overall aggregated communities across years on density loss (e.g., overall effects could be cancelled out by contrasting effects among years). To synthesize the model outputs and to increase interpretability of our data, we finally applied meta-analyses across the yearly models. However, as an add-on exercise, we also aggregated the abundances of the species and analyzed the overall communities.

In ecological studies, biases in sample completeness could influence a study's inference (Chao and Jost 2012). To account for potential sampling bias, we calculated for each log and year the sample coverage based estimated species diversity based on Hill (1973) numbers using the function *estimateD* from the R package 'iNEXT' (Hsieh et al. 2016). The Hill framework, which allows the calculation of diversity indices based on the Hill number, that assigns varying weights to species frequencies, has been widely utilized in community ecological research (Ellison 2010; Hill 1973). The Hill number of order $q=0$ corresponds to the presence/absence of species and thus gives more weight to species in the community with low frequencies such as rare species. This measure reflects species richness. The Hill number of order $q=1$ corresponds to Shannon diversity, representing the effective number of common species, while the Hill number of order $q=2$ corresponds to Simpson diversity, representing the effective number of dominant species.

This framework can also be applied for the analysis of the community composition and thus, beta diversity (Chao et al. 2014). Therefore, we calculated for all community matrices coverage-based dissimilarities along the Hill series using the function *iNEXTbeta3D* within the R package 'iNEXTbeta3D' (Chao and Hu 2024). The Chao-Sørensen index ($q=0$) treats all species equally and thus emphasizes rare species. The abundance-based Horn index ($q=1$), weights each species by its abundance and thus, reflects common species. Finally, the abundance-based Morisita-Horn index ($q=2$) is highly sensitive to dominant species and assigns little weight to rare species (Chiu and Chao 2014).

In a first step, we considered all environmental variables to test for the relative importance of canopy cover, deadwood heterogeneity, deadwood amount, tree species, and fungal alpha and beta diversity on deadwood density loss. Tree species (beech vs. fir) and canopy cover (open vs. closed) were treated as factors, while deadwood amount and deadwood heterogeneity were standardized (z-transformed) continuous predictors. However, from previous studies, we have evidence that host tree species is an important predictor for fungal alpha and beta diversity (Baber et al. 2016; Krah et al. 2018; Rieker et al. 2022). To avoid that fungal diversity effects on deadwood density loss is confounded by tree species, we analyzed our data separately for the tree species beech and fir. Note that the number of fir logs with fungal diversity measured via fruit body sampling in 2012 ($n=5$) was too low to calculate reliable results and was therefore excluded from the analyses.

We applied structural equation models (SEMs) using the *sem* function within the R package 'lavaan' (Rosseel 2012). These models were implemented separately for alpha and beta diversity. SEMs allowed us to examine both the direct effects of the environmental and fungal diversity on deadwood density loss and the indirect effects of the environment mediated by fungal species diversity. Deadwood density loss, expressed as a proportional response variable with values between 0 and 1, was arcsin-transformed to reach normal distribution. Species alpha diversity, which served as a second response variable and also as a predictor, was $\log_{10}$-transformed prior to analysis. At the beta diversity level, we conducted Principal Coordinates Analyses (PCoA) for each species dissimilarity matrix of each Hill number, using the *cmdscale* function from the R package 'stats'. We extracted the species scores for the first two axes of the Principal Coordinates Analyses as vector predictors representing community composition. These species scores were normally distributed and therefore did not require additional transformation within the SEMs. SEMs were applied separately for each annual combination of sampling method and diversity index ($q0$, $q1$, $q2$), covering both alpha diversity (estimated species diversity) and beta diversity (community composition).

In all models, we included site as an additional predictor to account for the nested design.

To synthesize results across years, we performed meta-analyses on the outputs of the annual alpha and beta SEMs. This was achieved using the *metagen* function from the R package 'meta' (Schwarzer et al. 2015), combining the estimates and standard errors of predictors from the annual models to generate overall effect sizes of the direct and indirect effects on deadwood density loss for each combination of sampling method and diversity index.

To check the robustness of the SEM models, we additionally applied single models. We specified a model for deadwood density loss as a response using the beta regression family (beta distributed data 0,1; *gam* function from the R package 'mgcv' (Wood 2015), specifying the argument 'family = betar(link = 'logit'). We used the same parametric predictors as in the SEM models. In addition, we considered site as a random effect in our models to account for the nested structure of our study design. Note that on six plots, we sampled both a beech and a fir object within the same plot. Conceptually, this would require specifying a random effect of plot nested within site. However, due to the very small numbers of plots with the sampling of two objects the models indicated singular fits. Nevertheless, the model performances were quite similar if specifying only site as a random effect. We, therefore, report only model outputs based on models using site as the random effect. We specified linear mixed-effects models using the *lmer* function from the R package 'lmerTest' (Kuznetsova et al. 2017). We used fungal diversity as the response, the environmental variables as predictors and considered site as a random effect. Effective number of species based on the Hill series are decimals and no count data. To reach normality, we $\log_{10}$-transformed estimated species diversity (for alpha diversity) and used the raw scores of the first two PCoA axes (for beta diversity) as these were normally distributed. As with the SEMs, these models were applied for each annual combination of sampling method and diversity index ($q0$, $q1$, $q2$).

As a final exercise, we aggregated the communities across years thereby summing the OTUs abundances. As reads from metabarcoding are not true species abundances, we used incidence data (i.e., abundance of an OTU is the number of years the OTU has been observed in our data set). Prior to aggregation, we rarefied (minimum read sum per sample: 887 (beech), 1129 (fir)) the complete yearly based community matrices to avoid biases (i.e., false probability of an OTU detected and thus false incidence and subsequently abundance caused by differences in sequencing depth among samples).

Results

After ten years of decomposition, log density loss ranged from 0.04% to 80% (Table S1). Annual models and meta-analyses based on both sampling methods consistently identified tree species identity as the primary driver of

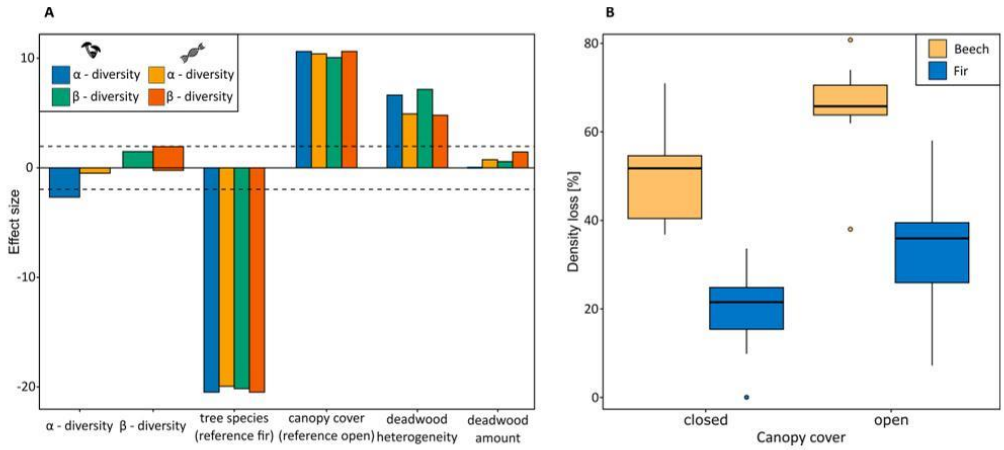

Fig. 2 **A**. Effect size (*z*-value) of environmental predictors on deadwood density loss for alpha and beta diversity ($q0$ values) for each sampling method, determined through meta-analyses based on the annual structural equation models. Dashed lines indicate the thresholds for significance (*z*-values: ± 1.96). **B**. Raw plots of density loss for each tree species (yellow: beech, blue: fir) in each canopy cover after ten years of decomposition

deadwood density loss, with significantly higher loss observed in beech logs compared to fir logs (Fig. 2, Table S2). Canopy cover showed also a high effect size on deadwood density loss with significantly higher density loss in logs located under open compared to closed canopies (Fig. 2, Table S2).

Effects of the environment on deadwood density loss

The tree species-based models identified canopy cover as significant and as the most important driver of deadwood density loss. This finding was mostly consistent across all annual models (Table S3, S5) and the models with across years aggregated data (Table S9, S10) at the alpha level and for most models at the beta level, irrespective of sampling method (metabarcoding or fruit body sampling) (Tables 1, 2; Fig. 3). An exception was observed for fruit body sampling on beech, where canopy cover emerged as the second most important driver (Table 1). Accordingly, density loss was higher under open canopies compared to closed canopies, aligning with the patterns observed in the raw data plots (Fig. S2).

Deadwood heterogeneity in the surrounding also affected deadwood density loss significantly for all three diversity measures ($q0$, $q1$, $q2$) at both the alpha and beta diversity levels for both sampling methods of beech, but not for fir, either in relation to the fruit body or metabarcoding data (Tables 1, 2; Table S3, S5). This pattern is also obvious in the raw plots (Fig. S3) and supported by the models with across years aggregated data (Table S9). Furthermore, it is supported by the annual models, except for beech metabarcoding data in the annual models 2015 (beta regression models; Table S3, S6) and 2021 (SEM; Table S5). Thus, beech logs on plots with high surrounding deadwood heterogeneity exhibited higher density loss than plots with lower surrounding deadwood heterogeneity (Table 1).

The surrounding deadwood amount had no significant effect on density loss of beech logs (Fig. 3). In contrast, deadwood amount showed significant effects on density loss of fir (Fig. 3). However, effect sizes are small, and significance was not consistent across all fir models (Table 2). Annual models revealed that effects were caused by one single year. Further, effects on fir logs based on the meta-analysis were either absent in the annual models (fir metabarcoding) or occurred only in one single year (e.g., 2013, fir fruit body sampling) (Table S3, S5, S6, S8).

Effects of fungal diversity on deadwood density loss

We observed significant direct effects of fungal alpha diversity on deadwood density loss in both the metabarcoding and fruit body data for beech logs, as well as in the fruit body data for fir logs (Fig. 3). Higher richness of rare, common and dominant species detected by metabarcoding on beech logs was associated with higher density loss (Table 1). In contrast, higher richness of fruiting species was associated with reduced density loss (beech: $q2$; fir: $q0$, $q1$), indicating that higher fruiting species richness leads to slower density loss (Tables 1, 2). This effect is particularly evident for fir in the raw plots (Fig. 4). These findings are supported by at least one annual model (Table S3, S5), but only for fir in the models with across years aggregated data (Table S9). Effects of community dissimilarity on deadwood density loss based on the meta-analysis were not supported by the annual models, except for communities of common species detected via fruit body on beech logs (Fig. 4; Table S6, S8).

Effects of the environment on fungal diversity

The meta-analysis of the annual structural equation models indicate canopy cover as main driver of fungal diversity across tree species and sampling method (Fig. 3; Tables 1, 2). Fungal species alpha diversity of rare, common and dominant species, which were detected via metabarcoding on fir logs and via fruit body sampling on beech logs, showed higher effect sizes in open than in closed canopies (Tables 1, 2). However, this effect was weak when focusing on the raw plots (Fig. S4) and was significant only in one single year (2021 for fir metabarcoding, 2015 for beech fruit body sampling). Nevertheless, we found that canopy cover affects the dissimilarity levels of rare ($q0$) and common ($q1$) species communities (Tables 1, 2). This finding is further supported by the models using data aggregated across years (Table S10), whereas dissimilarity levels of dominant species communities ($q2$) were not affected by canopy cover (except for communities detected on fir logs via fruit body sampling). These patterns with mainly effects on dissimilarities of rare and common species communities were supported by the most annual models (LMER and SEM) and raw plots (Table S7, S8; Fig. S5).

Deadwood heterogeneity had minor effects on fungal diversity at either alpha or beta diversity level (Fig. 3). An exception was found for the alpha diversity of rare species detected via fruit body sampling on fir logs where deadwood heterogeneity showed a positive effect. Furthermore, deadwood heterogeneity showed a significant effect on the dissimilarity of dominant species communities found on beech logs via metabarcoding and on fir logs via fruit body sampling (Fig. 3). However, the annual models (LMER and SEM) showed only effects in single years (Table S4, S5, S7, S8).

The surrounding deadwood amount showed weak positive effects on alpha diversity level on rare, common and dominant species diversity detected via fruit body sampling on beech logs with higher diversity on

Table 1 Effect sizes (*z*-values) of the meta-analyses of the structural equation models for alpha and beta diversity levels for each diversity measure based on Hill numbers (*q*0, *q*1, *q*2) on beech logs. Three structural equation models, each for alpha and beta diversity, were performed for each sampling method: (a) based on metabarcoding fungal data; (b) based on fungal fruit body data. Upward-pointing arrows for the predictors deadwood heterogeneity and amount indicate that the reference is based on increasing values, implying that if the *z*-value is positive, an increase in heterogeneity or amount would also increase density loss or fungal diversity. For beta diversity, fungal community composition was represented by the first two axes of a Principal Coordinates Analysis (first axis: PCoA1; second axis: PCoA2). Significant effects of the SEM meta-analysis are those that exceed the critical value of the *z*-test ($-1.96 < z > 1.96$) and are indicated in bold. Values are shown in parentheses if they are not significant in at least one year based on the yearly-based SEM analyses and thus not considered significant within our interpretation. Note that we arcsin-transformed density loss and $\log_{10}$-transformed alpha diversity prior to analyses (see Materials and methods section for more detail)

				Canopy cover = 'open'	Deadwood heterogeneity = ↑	Deadwood amount = ↑	Fungal diversity
a) Beech metabarcoding							
Alpha	*q*0-model	Diversity		0.80	1.21	0.44	–
		Density loss		**7.42**	**6.29**	0.68	**2.83**
	*q*1-model	Diversity		− 0.37	1.14	1.01	–
		Density loss		**8.98**	**6.07**	0.45	**3.25**
	*q*2-model	Diversity		− 0.87	1.10	1.33	–
		Density loss		**9.90**	**6.07**	0.14	**2.59**
Beta	*q*0-model	Diversity	PCoA1	**6.59**	1.11	− 0.67	
			PCoA2	− 1.22	− 0.04	− 0.32	
		Density loss	PCoA1	**5.49**	**6.71**	**(2.01)**	1.57
			PCoA2				1.38
	*q*1-model	Diversity	PCoA1	**3.17**	1.82	0.36	
			PCoA2	1.85	0.41	0.22	
		Density loss	PCoA1	**6.36**	**6.44**	1.19	0.72
			PCoA2				− 0.46
	*q*2-model	Diversity	PCoA1	− 0.76	1.49	− 0.46	
			PCoA2	1.93	− **2.26**	1.36	
		Density loss	PCoA1	**8.75**	**7.52**	0.43	0.71
			PCoA2				− 0.68
b) Beech fruit body							
Alpha	*q*0-model	Diversity		**3.37**	− 1.15	**3.24**	–
		Density loss		**7.80**	**8.32**	0.54	**(− 2.61)**
	*q*1-model	Diversity		**3.52**	− 1.19	**3.33**	–
		Density loss		**7.87**	**8.35**	0.52	**(− 2.67)**
	*q*2-model	Diversity		**3.69**	− 1.17	**3.30**	–
		Density loss		**7.96**	**8.41**	0.50	**− 2.77**
Beta	*q*0-model	Diversity	PCoA1	**7.47**	− 0.25	0.68	
			PCoA2	1.15	0.59	-0.96	
		Density loss	PCoA1	**5.49**	**9.05**	0.70	1.75
			PCoA2				1.74
	*q*1-model	Diversity	PCoA1	**9.06**	− 0.49	1.12	
			PCoA2	1.26	1.09	**(− 3.11)**	
		Density loss	PCoA1	**6.97**	**8.59**	1.47	**2.04**
			PCoA2				− 1.51
	*q*2-model	Diversity	PCoA1	− 0.38	0.00	− 0.96	
			PCoA2	− 0.18	0.04	− 0.61	
		Density loss	PCoA1	**8.01**	**9.52**	0.33	**(− 2.57)**
			PCoA2				0.78

logs with higher surrounding deadwood amount (Fig. 3, Table 1). By contrast, the opposite pattern was observed for species detected via fruit body sampling on fir logs, where surrounding deadwood amount had weak negative

Table 2 Effect sizes (*z*-values) of the meta-analyses of the structural equation models for alpha and beta diversity levels for each diversity measure based on Hill numbers (*q*0, *q*1, *q*2) on fir logs. Three structural equation models, each for alpha and beta diversity, were performed for each sampling method: (a) based on metabarcoding fungal data; (b) based on fungal fruit body data. Upward-pointing arrows for the predictors deadwood heterogeneity and amount indicate that the reference is based on increasing values, implying that if the *z*-value is positive, an increase in heterogeneity or amount would also increase density loss or fungal diversity. For beta diversity, fungal community composition was represented by the first two axes of a principal coordinates analysis (first axis: PCoA1; second axis: PCoA2). Significant effects of the SEM meta-analysis are those that exceed the critical value of the *z*-test (– 1.96 < *z* > 1.96) and are indicated in bold. Values are shown in parentheses if they are not significant in at least one year based on the yearly-based SEM analyses and thus not considered significant within our interpretation. Note that we arcsin-transformed density loss and $\log_{10}$-transformed alpha diversity prior to analyses (see Materials and methods section for more detail)

				Canopy cover = 'open'	Deadwood heterogeneity = ↑	Deadwood amount = ↑	Fungal diversity
a) Fir metabarcoding							
Alpha	*q*0-model	Diversity		**2.12**	– 0.77	1.54	–
		Density loss		**5.67**	– 0.23	**(2.43)**	**(– 2.08)**
	*q*1-model	Diversity		**2.66**	– 0.39	1.54	–
		Density loss		**5.56**	0.05	**(2.34)**	– 1.88
	*q*2-model	Diversity		**2.50**	0.08	1.42	–
		Density loss		**5.52**	– 0.07	**(2.43)**	– 1.55
Beta	*q*0-model	Diversity	PCoA1	**14.42**	0.41	– 0.80	
			PCoA2	**2.71**	0.65	0.43	
		Density loss	PCoA1	**4.23**	– 0.82	**(2.98)**	0.44
			PCoA2				– 0.26
	*q*1-model	Diversity	PCoA1	**3.20**	0.89	– 0.73	
			PCoA2	1.01	0.01	0.34	
		Density loss	PCoA1	**5.70**	– 0.75	**(2.56)**	– 0.20
			PCoA2				**(– 2.66)**
	*q*2-model	Diversity	PCoA1	0.58	– 0.37	0.20	
			PCoA2	– 0.81	– 0.49	1.94	
		Density loss	PCoA1	**5.56**	– 0.67	**(2.60)**	0.19
			PCoA2				– 0.98
b) Fir fruit body							
Alpha	*q*0-model	Diversity		1.29	**1.97**	**– 2.28**	–
		Density loss		**4.58**	– 0.12	1.76	**– 2.06**
	*q*1-model	Diversity		1.25	1.95	**– 2.27**	–
		Density loss		**4.57**	– 0.13	1.76	**– 2.01**
	*q*2-model	Diversity		1.20	1.93	**– 2.26**	–
		Density loss		**4.54**	– 0.14	1.75	– 1.94
Beta	*q*0-model	Diversity	PCoA1	**2.28**	– 0.56	– 0.89	
			PCoA2	1.78	0.05	– 0.27	
		Density loss	PCoA1	1.57	– 1.67	**3.77**	1.00
			PCoA2				– 0.42
	*q*1-model	Diversity	PCoA1	**4.23**	– 1.37	0.00	
			PCoA2	– 1.09	0.80	– 0.12	
		Density loss	PCoA1	1.84	– 1.49	**(3.32)**	– 0.26
			PCoA2				– 1.96
	*q*2-model	Diversity	PCoA1	1.60	– 0.30	– 0.24	
			PCoA2	**3.09**	**2.31**	**– 3.06**	
		Density loss	PCoA1	**3.41**	– 1.05	2.42	0.66
			PCoA2				– 0.39

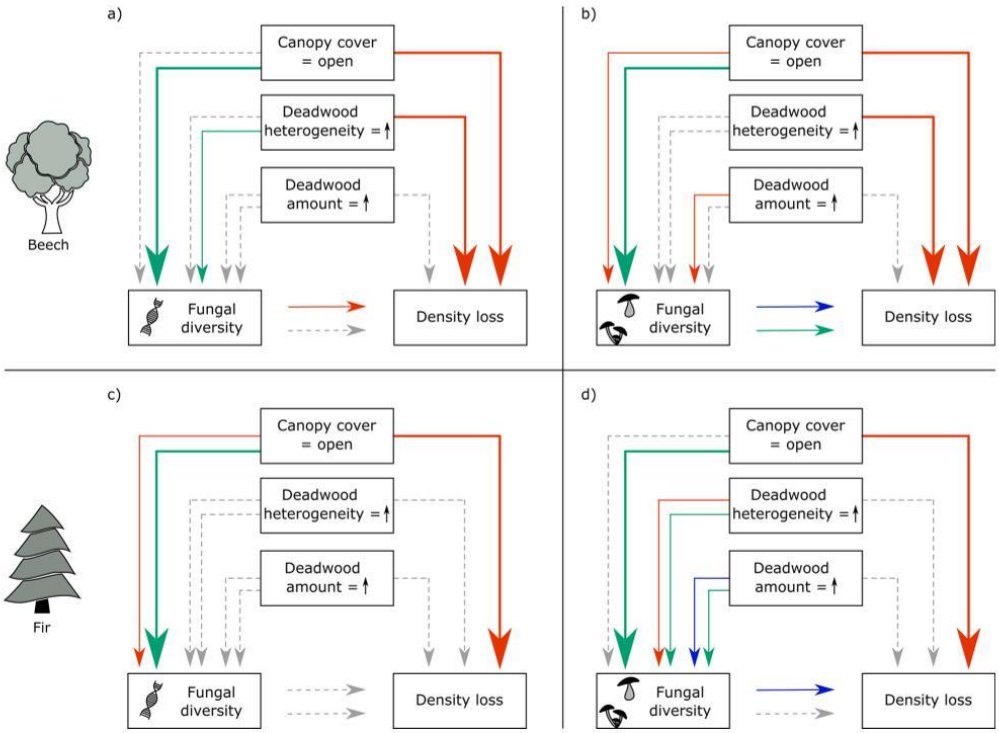

Fig. 3 Compiled illustrated results based on the meta-analyses of the structural equation models for alpha and beta diversity levels for tree species (beech, first row **a**) and **b**); fir second row **c**) and **d**)) and sampling method (metabarcoding, first column **a**) and **c**); fruit body, second column **b**) and **d**)). Please refer to Table 1 & 2 for detailed effects and Method section for exact descriptions. For alpha diversity, the red color indicates a significant positive and the blue color a significant negative relationship. For beta diversity, the significant relationships are indicated by the green color. The colored arrows represent combined effects across three diversity measures (*q*0, *q*1, *q*2), with significance assigned if at least one measure showed a significant effect. Thick arrows represent stronger effects sizes (> 4.0). Non-significant relationships are indicated by the gray dashed line. The relationships between environmental variables and density loss are grouped across models (one single arrow), considered significant if at least half of the alpha and beta models showed significance, and drawn as thick arrows if at least half of these had effect sizes > 4.0 (see Tables 1 & 2)

(See figure on next page.)

Fig. 4 Deadwood density loss in relation to **A** estimated species richness (alpha diversity) and **B** community composition (beta diversity, represented by the first two axes of a principal coordinates analysis (PCoA 1, PCoA 2)) for rare ($q = 0$), common ($q = 1$), and dominant ($q = 2$) species on beech and fir deadwood. Fungal diversity was assessed using two methods: fruit body surveys (fungal pictogram) and metabarcoding (DNA double helix pictogram). Solid lines denote significant, and dashed lines non-significant, effect sizes from meta-analyses of the structural equation models (see caption of Fig. 3, Tables 1 and 2)

effects on the alpha diversity of rare, common, and dominant species (Table 2). However, these patterns were supported by only single annual models but not by the models with across years aggregated data or the raw data plots (Table S4, S5, S7, S8, S9, S10; Fig. S6). Similarly, this issue was observed in the dissimilarity of communities of common species (on beech logs) and community dissimilarity of dominant species (on fir logs) (Tables 1, 2).

Discussion

Overall, density loss was mainly explained by tree species and canopy cover. Beech showed stronger density loss than fir and density loss was higher under open compared to closed canopies.

For both tree species, density loss was better explained by canopy cover than fungal alpha and beta diversity. The effects of fungal diversity were

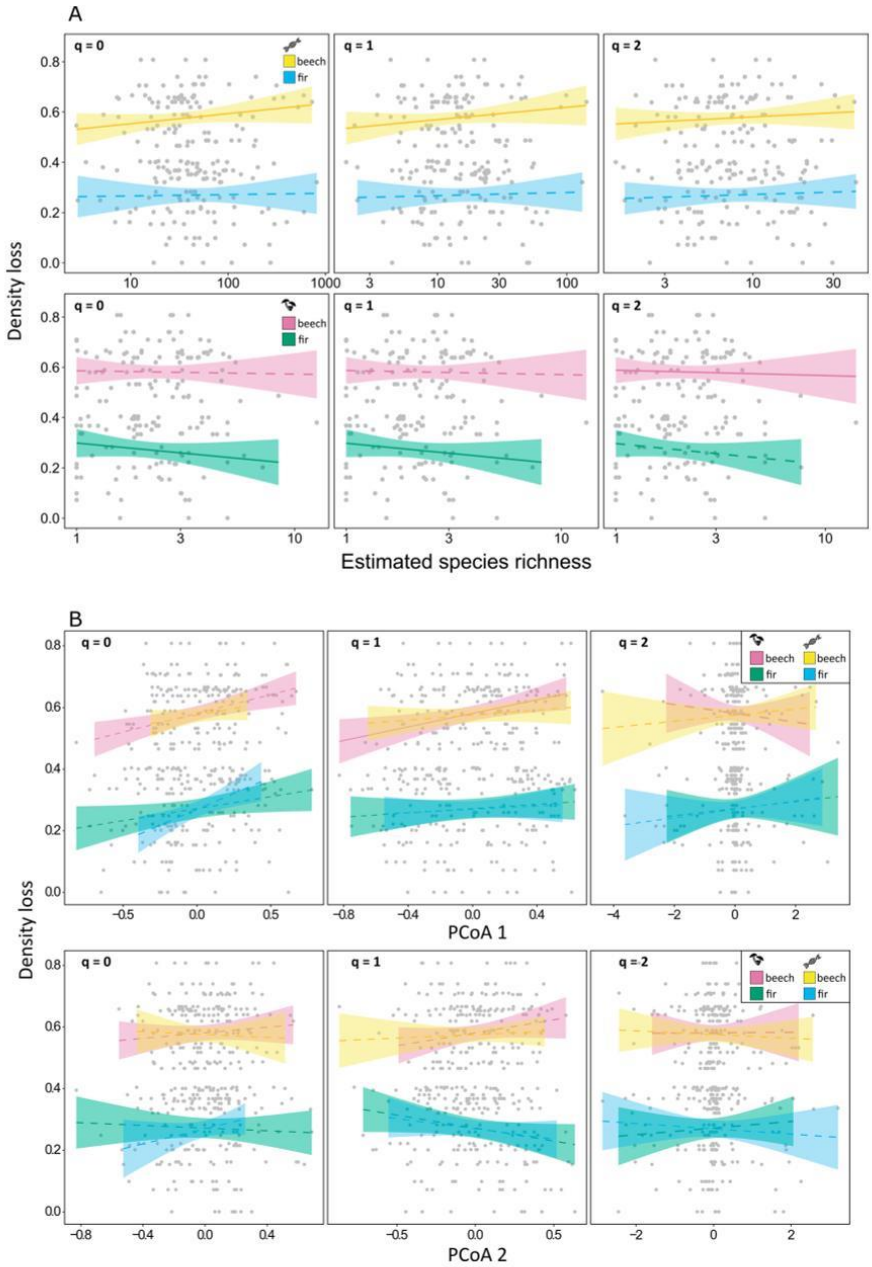

Fig. 4 (See legend on previous page.)

inconsistent across tree species, diversity measures and model approaches.

Effects of the tree species and stand-scale factors on deadwood density loss

Our overall models showed that among all predictors, tree species was the main factor explaining deadwood density loss. Tree species as major driver of deadwood decomposition is well studied (Harmon et al. 2020; Kahl et al. 2017; Kipping et al. 2022; Shorohova and Kapitsa 2014; Weedon et al. 2009). Our results are in line with these studies, showing higher decomposition rates in angiosperm wood compared to gymnosperm wood, which can be mainly explained by differences in their wood traits. Gymnosperms exhibit a higher concentration of lignin and lower levels of nitrogen and phosphorus, contributing to their slower decomposition rates compared to angiosperms (Weedon et al. 2009). Additionally, the structural composition of lignin differs between gymnosperms and angiosperms. Angiosperm lignin contains a higher proportion of sinapyl moieties (structural elements derived from sinapyl alcohol), which form less densely cross-linked networks compared to guaiacyl moieties (structural elements derived from coniferyl alcohol) found predominantly in gymnosperm lignin (Brunow 2001; Hatakka and Hammel 2010; Higuchi 2006). As a result, angiosperm lignin is more susceptible to chemical and enzymatic degradation. Furthermore, angiosperm and gymnosperm wood also differ in characteristics such as the composition of hemicellulose and variations in structural compounds within tracheids, which may influence decomposition processes (Weedon et al. 2009). Thus, based on prior knowledge and the results of our study, we can conclude that tree species outperform even considerable variability in environmental condition (e.g., microclimate) and fungal diversity pattern in explaining deadwood density loss.

In addition to tree species identity, our overall models identified canopy cover as the second most important predictor explaining deadwood density loss. Moreover, it was the strongest predictor in most of the tree species-specific models. Our findings with higher density losses under open canopies have been reported before (Harmon et al. 2020; Janisch et al. 2005; Shorohova and Kapitsa 2014). However, in our study, we were able to rule out potential masked effects by fungal diversity. Thus, reasons for the observed effects might be that open canopy conditions expose deadwood logs to more solar radiation and thus accelerates photodegradation and surface degradation (Derbyshire and Miller 1981; George et al. 2005). Surface degradation can be further enhanced by physical processes, such as frost cracking, which are influenced by greater temperature variability in open canopy conditions (Fravolini et al. 2018; Harmon et al. 1986; Russell et al. 2015; Zhou et al. 2007). Furthermore, increased solar radiation can enhance degradation of specific wood components, such as lignin, thereby improving enzymatic accessibility for microorganisms and potentially accelerating deadwood decomposition (Austin et al. 2016). These potential direct mechanisms caused by open canopies are supported by the fact that we observed rather weak indirect effects via fungal diversity. Even though the fungal communities were consistently affected by canopy cover, the effects of the fungal communities on density loss were weak (see also discussion below). However, the study by Janisch et al. (2005) found only minor differences in decomposition rates between open and closed canopies. This may be attributed to their focus on the early stages of decomposition and the natural vegetation growth in the clearcuts, which provided shading and moisture during their study period. In our experiment, annual mowing ensured that the canopy cover remained open, preventing ground vegetation from shading the logs and disrupting the openness. Discrepancies among studies might also result from differences in macroclimatic conditions. Indeed, Harmon et al. (2020) suggested that the effect of canopy cover may interact with macroclimatic conditions. For instance, moisture availability, which depends on precipitation level, could either enhance or inhibit deadwood decomposition, depending on whether it becomes a limiting factor (Seibold et al. 2021). Our study area is characterized by a high level of precipitation and thus, moisture is most probably not limiting. Nevertheless, more studies are needed to disentangle interactions between macro- and microclimate considering both, temperature and moisture availability.

Our results showed that the heterogeneity of the surrounding deadwood affects directly deadwood density loss with higher heterogeneity associated with higher deadwood density losses in beech. It is noteworthy that this could be not a masked effect of the fungal diversity as we tested heterogeneity directly and indirectly (via diversity) in one model. Thus, the theoretical assumption that diversity increases with habitat heterogeneity and thus affects density loss via diversity increase is not supported here. We can only speculate about the mechanisms, why deadwood heterogeneity in the surrounding increases density loss in beech. One explanation might be that beech objects are characterized by additional fir logs on plots with a high level of heterogeneity. The existence of fir might affect small-scale microclimate conditions on the plot beyond canopy cover. The decomposition level of fir is lower than that of beech in our setting. Even though we have no data, own observations suggest that

the bark cover of fir is larger than in beech. Further, fir with remaining bark appears darker than debarked beech wood, which is additionally often characterized by white rot. Thus, fir on a plot could increase microclimate temperature and potentially explain an increased density loss, e.g. via increased metabolic rate. However, this remains speculative, and more microclimate and metabolic data would be needed to disentangle microclimate effects beyond canopy cover on density loss.

Effects of fungal diversity measures on density loss

We found some significant effects of fungal diversity on density loss. However, effect sizes were mostly weak and smaller than those observed for the environmental effects. Furthermore, we found mostly inconsistent effects across tree species, diversity measures and model approaches. Several studies in the past focused on the fungal diversity–decomposition relationship in chronosequence approaches (Rajala et al. 2011; van der Wal et al. 2015; Yang et al. 2024). However, summarized across studies, it has been recently demonstrated that there is no consensus about the relationship between wood-inhabiting fungal diversity and decomposition processes (Runnel et al. 2025). It has been, therefore, suggested that novel approaches are needed considering real world settings with natural communities considering a broad range of diversity measures and importantly, considering both direct and indirect effects of the environment. With our study, we contribute to close one knowledge gap in fungal biodiversity–ecosystem functioning (BEF) research and demonstrated that environmental variability outperforms fungal diversity in explaining deadwood density loss as an important ecosystem process in forest ecosystems. This holds true for a broad range of diversity measures that is, alpha and beta diversity and particularly whether we consider rare, common or dominant species. We suggest that from an extremely diverse species pool in a landscape, distinct communities assemble under certain environmental conditions that are functionally redundant and thus always equipped with the capability (e.g., wood degrading enzymes) to decompose wood. This has been clearly revealed by our structural equation models showing that the fungal communities on beech and fir based on both, fruit bodies and metabarcoding were strongly affected by canopy cover but in turn, the community compositions were weakly related to density loss. However, to gain more mechanistic insights about how fungal communities decompose wood under specific environmental conditions, more studies are needed characterizing the active communities (e.g., via RNA), the real abundance (i.e., fungal biomass) and functional performance of fungi individuals (e.g., via proteomics (Kipping et al. 2024)) in deadwood under specific environmental conditions.

Limitations

First, we have only one deadwood density measure value after ten years. This limits our ability to gain insights about year-to-year decomposition dynamics. However, our data showed that after ten years, deadwood density loss is up to 80%. This indicates that the variability in decomposition is close to the maximum range in our study and thus, allowed us to analyze a broad range of decomposition without losing data (i.e., fully decayed logs after > 10 years). Second, we calculated density loss using literature-derived baseline values, as no initial samples of the logs were taken at the start of the experiment. This might cause imprecise density values. For example, if the density of the wood is exceptional, e.g., due to competitive growth conditions, density loss can be underestimated. This might explain one low density loss value (< 0.1%) observed for a fir log. However, the variability of density among our logs was considerable and we, therefore, safely assume that this variability is mainly caused by the abiotic and biotic factors in our setting. Third, density loss was examined by measuring and calculating the density based on log disk subsamples from the edges assumed to represent the entire log. However, it is well known that the decomposition of coarse woody debris can be spatially quite heterogeneous (Pyle and Brown 1999). Nevertheless, we tried to account for this by first cutting a slice from the edges before cutting the final disc and due to the number of replicates. Fourth, we used deadwood density loss as a proxy for deadwood decomposition, although this metric may underestimate certain aspects of decay dynamics (Petrillo et al. 2016). Deadwood density also does not account for wood loss from the outer log space (e.g., sapwood loss). Thus, other measures, such as changes in lignin and cellulose concentrations, may provide additional insights of decomposition processes (Fravolini et al. 2018; Lombardi et al. 2013). However, density loss remains a clearcut and practical, easy to measure parameter used in comparable studies (Rajala et al. 2011; van der Wal et al. 2015; Yang et al. 2024).

Conclusions

Deadwood decomposition is primarily driven by tree species identity and canopy cover, while fungal diversity plays a minor role. This suggests that the carbon and nutrient cycle in temperate forests is mainly affected by forest management decisions via tree species choice and logging intensity affecting the canopy. More specifically, transformation of forest ecosystems towards angiosperm trees and increased canopy disturbance, both forced by global warming, might cause higher rates of deadwood turnover. Consequently, carbon sequestration is expected to decrease, and atmospheric carbon release is expected

to increase in temperate forest ecosystems in the future. Further research is needed to disentangle the effects of other factors, such as moisture content, which is a key determinant for both deadwood decomposition and fungal growth and, also expected to change considerably with global warming (Coppola et al. 2021). Understanding these interactions could provide deeper insights into the mechanisms underlying decomposition processes and their drivers, which is precondition for carbon cycle modelling and upscaling in times of climate change.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-025-00619-8.

Supplementary Material 1.

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Author contributions
CB, PB designed the concept of the study. JS and CB analyzed, interpreted and wrote the manuscript. PB, VB, HK, FR and MS helped with the writing of the final manuscript.

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Availability of data and materials
The datasets generated and/or analysed during the current study are available in the SRA archive repository, https://www.ncbi.nlm.nih.gov/sra, PRJNA1231988.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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Publisher's Note

"Effects of canopy-mediated microclimate and object characteristics on deadwood temperature"

Supplementary Information

T0ab. S1 List of the 42 deadwood objects for which the density loss was measured after ten years of decomposition, along with their corresponding object and environmental characteristics.

Object	Block	Plot	Surrounding deadwood [m^3/ha]	Surrounding deadwood heterogeneity	Tree species	Canopy cover	Density [g/cm^3]	Density loss [%]
AG01-004-B-C	A	AG01	176.25	1	beech	shady	0.41	40.04
AG02-008-T-C	A	AG02	103.27	1	fir	shady	0.37	9.86
AG19-089-B-C	A	AG19	161.46	4	beech	shady	0.31	54.61
AG19-091-T-C	A	AG19	161.46	4	fir	shady	0.27	33.65
AO01-098-B-C	A	AO01	139.99	1	beech	sunny	0.25	63.81
AO02-101-T-C	A	AO02	128.29	1	fir	sunny	0.26	36.73
AO08-130-T-C	A	AO08	145.56	2	fir	sunny	0.25	39.48
BG01-195-B-C	B	BG01	170.98	1	beech	shady	0.36	46.56
BG02-200-T-C	B	BG02	116.01	1	fir	shady	0.32	22.19
BG07-224-B-C	B	BG07	207.51	2	beech	shady	0.32	53.27
BG08-230-B-C	B	BG08	159.56	2	beech	shady	0.35	48.16
BG08-231-T-C	B	BG08	159.56	2	fir	shady	0.33	20.12
BG11-243-T-C	B	BG11	168.75	4	fir	shady	0.35	15.39
BO01-291-B-C	B	BO01	125.82	1	beech	sunny	0.20	70.54
BO02-294-T-C	B	BO02	139.21	1	fir	sunny	0.26	35.94
BO03-298-B-C	B	BO03	134.14	2	beech	sunny	0.23	66.61
BO07-316-B-C	B	BO07	186.99	2	beech	sunny	0.24	65.26
BO09-329-B-C	B	BO09	165.20	4	beech	sunny	0.13	80.76
DG03-588-T-C	D	DG03	181.66	2	fir	shady	0.28	32.07
DG06-599-B-C	D	DG06	193.43	1	beech	shady	0.41	40.44
DG09-616-B-C	D	DG09	221.16	2	beech	shady	0.20	71.00
DG14-644-T-C	D	DG14	190.00	4	fir	shady	0.32	21.52
DG16-654-T-C	D	DG16	122.07	1	fir	shady	0.29	28.24
DO01-676-T-C	D	DO01	157.48	2	fir	sunny	0.38	7.21
DO04-687-T-C	D	DO04	139.74	1	fir	sunny	0.27	33.34
DO05-691-B-C	D	DO05	189.95	1	beech	sunny	0.42	38.00
DO06-695-B-C	D	DO06	196.73	2	beech	sunny	0.23	65.87
DO13-733-B-C	D	DO13	176.48	2	beech	sunny	0.26	61.92
DO13-736-T-C	D	DO13	176.48	2	fir	sunny	0.27	35.18
EG07-795-B-C	E	EG07	138.06	1	beech	shady	0.43	36.80
EG10-807-T-C	E	EG10	174.63	2	fir	shady	0.31	24.84
EG12-821-T-C	E	EG12	186.51	1	fir	shady	0.41	0.04
EG16-845-B-C	E	EG16	231.35	2	beech	shady	0.28	58.90
EG17-854-B-C	E	EG17	149.04	2	beech	shady	0.33	51.77
EG17-855-T-C	E	EG17	149.04	2	fir	shady	0.34	16.19
EO01-868-T-C	E	EO01	192.65	2	fir	sunny	0.30	25.93
EO02-875-T-C	E	EO02	176.01	1	fir	sunny	0.17	58.02
EO06-895-B-C	E	EO06	140.29	1	beech	sunny	0.23	65.77
EO10-914-B-C	E	EO10	151.93	2	beech	sunny	0.24	64.01
EO10-915-T-C	E	EO10	151.93	2	fir	sunny	0.33	20.21
EO17-941-B-C	E	EO17	214.91	4	beech	sunny	0.18	73.99
EO17-943-T-C	E	EO17	214.91	4	fir	sunny	0.21	48.67

Tab. S2 Meta-analysis of annual structural equation models (SEM) of alpha (qD, estimated species richness) and beta diversity (ord1/2, community composition) based on both sampling methods (metabarcoding and fruit body data). Show that tree species is the most important factor for deadwood density loss. Community composition was represented by vector predictors using the species scores from the first two axes (Ord1, Ord2) of the Principal Coordinates Analyses (see Method section). The tilde represents the tested term (dependent variable ~ predictor variables). The following were tested: i) the influence of alpha/beta species diversity on deadwood density loss, ii) the influence of environmental variables on deadwood density loss, iii) the influence of environmental variables on alpha/beta species diversity. Models were conducted for each combination of sampling method and diversity measures. Bold values indicate significant effects (p-value < 0.05).

				qD		Tree species = fir		Canopy = open		Deadwood heterogeneity		Deadwood amount	
				z	p	z	p	z	p	z	p	z	p
Alpha diversity	Metabarcoding	i) Loss ~ qD	q0	-0.06	0.951								
			q1	-0.27	0.784								
			q2	-0.49	0.625								
		ii) Loss ~ env	q0			**-18.77**	0.000	**9.40**	0.000	**4.80**	0.000	0.69	0.493
			q1			**-19.62**	0.000	**10.06**	0.000	**4.97**	0.000	0.65	0.518
			q2			**-19.93**	0.000	**10.40**	0.000	**4.92**	0.000	0.75	0.456
		iii) qD ~ env	q0			**5.88**	0.000	1.96	0.050	0.08	0.933	0.96	0.335
			q1			**3.61**	0.000	**2.28**	0.023	0.04	0.972	1.73	0.083
			q2			**2.23**	0.025	1.89	0.058	0.24	0.808	2.17	0.030
	Fruit body	i) Loss ~ qD	q0	**-2.69**	0.007								
			q1	**-2.64**	0.008								
			q2	**-2.59**	0.010								
		ii) Loss ~ env	q0			**-19.98**	0.000	**10.64**	0.000	**6.44**	0.000	0.10	0.918
			q1			**-20.21**	0.000	**10.62**	0.000	**6.52**	0.000	0.01	0.995

			q2					**-20.48**	0.000	**10.62**	0.000	**6.64**	0.000	-0.08	0.933
		iii) qD ~ env	q0					-1.02	0.309	**2.00**	0.045	-0.39	0.696	1.12	0.265
			q1					-0.98	0.326	**2.15**	0.032	-0.60	0.547	1.14	0.252
			q2					-0.97	0.332	**2.26**	0.024	-0.71	0.475	1.09	0.275
				Ord1		Ord2									
				z	p	z	p								
Beta diversity	Metabarcoding	i) Loss ~ Ord	q0	-0.06	0.952	1.94	0.053								
			q1	1.61	0.107	0.28	0.780								
			q2	-0.24	0.811	0.32	0.750								
		ii) Loss ~ env	q0					**-10.51**	0.000	**5.87**	0.000	**4.13**	0.000	1.44	0.150
			q1					**-10.86**	0.000	**8.53**	0.000	**4.44**	0.000	1.21	0.225
			q2					**-20.48**	0.000	**10.63**	0.000	**4.80**	0.000	0.93	0.352
		iii) Ord1 ~ env	q0					**-11.19**	0.000	**3.26**	0.001	0.26	0.794	0.79	0.430
			q1					**-33.20**	0.000	**2.68**	0.007	-0.37	0.713	1.00	0.317
			q2					-0.33	0.744	-0.24	0.814	**2.08**	0.038	-1.45	0.148
		iii) Ord2 ~ env	q0					**-8.11**	0.000	**18.32**	0.000	**2.20**	0.028	-1.53	0.126
			q1					1.68	0.092	0.95	0.345	-1.45	0.147	0.51	0.610
			q2					0.50	0.616	-0.30	0.767	-0.18	0.855	1.10	0.273
	Fruit body	i) Loss ~ Ord	q0	0.46	0.643	0.18	0.860								
			q1	1.48	0.138	0.60	0.549								
			q2	0.15	0.877	-0.04	0.966								
		ii) Loss ~ env	q0					**-7.08**	0.000	**6.53**	0.000	**7.15**	0.000	0.12	0.902

			q1					**-6.66**	0.000	**8.16**	0.000	**6.38**	0.000	0.10	0.922
			q2					**-20.15**	0.000	**10.07**	0.000	**6.12**	0.000	0.57	0.570
		iii) Ord1 ~ env	q0					**-21.40**	0.000	**-4.80**	0.000	-0.42	0.673	-0.03	0.972
			q1					**-40.32**	0.000	**-3.17**	0.002	-0.46	0.648	0.45	0.651
			q2					-0.08	0.933	-0.76	0.445	0.74	0.460	-0.80	0.424
		iii) Ord2 ~ env	q0					-0.23	0.821	**4.11**	0.000	1.50	0.133	-1.46	0.143
			q1					0.51	0.607	0.26	0.795	1.31	0.190	-0.58	0.561
			q2					0.02	0.982	-0.53	0.599	-0.69	0.487	0.31	0.756

Tab. S3 Annual beta regression model illustrating the influence of environmental factors and alpha species diversity (qD, estimated species richness) on deadwood density loss. Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, z= z-value, p= p-value.

α – **beta regression model**			Species diversity				Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
			Est	se	z	p	Est	se	z	p	Est	se	z	p	Est	se	z	p
Beech Metabarcoding	2012	q0	0.37	0.38	0.99	0.323	0.71	0.27	**2.58**	0.010	0.37	0.13	**2.86**	0.004	0.03	0.13	0.21	0.836
		q1	0.46	0.52	0.90	0.369	0.73	0.27	**2.73**	0.006	0.38	0.13	**2.87**	0.004	0.03	0.13	0.22	0.826
		q2	0.53	0.63	0.84	0.401	0.76	0.26	**2.92**	0.004	0.38	0.13	**2.85**	0.004	0.04	0.13	0.27	0.789
	2013	q0	0.04	0.60	0.07	0.947	0.76	0.30	**2.57**	0.010	0.34	0.12	**2.90**	0.004	0.04	0.12	0.30	0.761
		q1	0.13	0.72	0.18	0.859	0.78	0.27	**2.88**	0.004	0.34	0.12	**2.90**	0.004	0.03	0.12	0.30	0.766
		q2	0.07	0.71	0.10	0.922	0.76	0.25	**3.06**	0.002	0.34	0.12	**2.89**	0.004	0.03	0.12	0.29	0.771
	2015	q0	0.13	0.47	0.27	0.786	0.65	0.30	**2.21**	0.027	0.24	0.12	1.91	0.056	0.06	0.11	0.54	0.587
		q1	-0.19	0.46	-0.40	0.686	0.76	0.25	**3.01**	0.003	0.25	0.12	**2.00**	0.046	0.06	0.11	0.53	0.595
		q2	-0.30	0.40	-0.75	0.451	0.74	0.22	**3.37**	0.001	0.25	0.12	**2.03**	0.042	0.06	0.11	0.58	0.560
	2018	q0	0.12	0.72	0.17	0.864	0.73	0.25	**2.94**	0.003	0.34	0.12	**2.88**	0.004	0.03	0.13	0.21	0.835
		q1	0.13	0.74	0.17	0.862	0.74	0.24	**3.11**	0.002	0.34	0.12	**2.88**	0.004	0.02	0.13	0.19	0.847
		q2	-0.02	0.69	-0.04	0.971	0.75	0.23	**3.25**	0.001	0.34	0.12	**2.90**	0.004	0.04	0.12	0.29	0.772
	2021	q0	1.13	0.38	**3.01**	0.003	0.74	0.19	**3.97**	0.000	0.24	0.10	**2.29**	0.022	0.04	0.10	0.45	0.656
		q1	1.63	0.42	**3.92**	0.000	0.85	0.17	**5.03**	0.000	0.19	0.10	**1.98**	0.048	0.02	0.09	0.24	0.811
		q2	1.86	0.47	**3.94**	0.000	0.95	0.17	**5.47**	0.000	0.18	0.10	1.93	0.054	-0.02	0.09	-0.26	0.795
		q0	-0.84	0.63	-1.33	0.183	1.23	0.44	**2.82**	0.005	0.37	0.24	1.58	0.113	-0.23	0.24	-0.96	0.337

Fir Metabarcoding	2012	q1	-0.87	0.73	-1.19	0.233	1.15	0.41	**2.76**	0.006	0.38	0.24	1.61	0.108	-0.16	0.23	-0.69	0.491
		q2	-0.74	0.80	-0.93	0.354	1.06	0.40	**2.67**	0.008	0.37	0.23	1.58	0.113	-0.13	0.24	-0.55	0.583
	2013	q0	-1.94	1.01	-1.93	0.054	0.86	0.36	**2.37**	0.018	0.27	0.22	1.22	0.222	-0.05	0.23	-0.23	0.815
		q1	-1.04	0.89	-1.17	0.243	0.96	0.38	**2.54**	0.011	0.28	0.23	1.21	0.226	-0.07	0.25	-0.28	0.783
		q2	-0.59	0.81	-0.73	0.466	0.98	0.38	**2.56**	0.010	0.30	0.24	1.28	0.201	-0.11	0.26	-0.44	0.663
	2015	q0	-0.76	0.52	-1.45	0.146	0.93	0.36	**2.55**	0.011	0.44	0.23	1.93	0.054	-0.16	0.23	-0.70	0.484
		q1	-1.15	0.60	-1.92	0.055	0.90	0.36	**2.49**	0.013	0.44	0.22	**2.00**	0.045	-0.12	0.23	-0.54	0.593
		q2	-1.17	0.60	-1.94	0.052	0.92	0.36	**2.56**	0.011	0.41	0.22	1.90	0.057	-0.12	0.23	-0.51	0.608
	2018	q0	0.65	0.90	0.73	0.468	0.85	0.40	**2.13**	0.034	0.42	0.24	1.77	0.076	-0.26	0.23	-1.14	0.255
		q1	0.92	0.80	1.15	0.249	0.82	0.39	**2.10**	0.036	0.48	0.25	1.93	0.054	-0.28	0.23	-1.24	0.214
		q2	0.88	0.70	1.27	0.205	0.83	0.38	**2.15**	0.031	0.46	0.24	1.88	0.060	-0.29	0.23	-1.25	0.212
	2021	q0	-0.74	0.56	-1.32	0.185	1.41	0.50	**2.82**	0.005	0.44	0.24	1.83	0.067	-0.30	0.24	-1.23	0.218
		q1	-0.81	0.72	-1.13	0.257	1.41	0.52	**2.73**	0.006	0.48	0.25	1.91	0.056	-0.31	0.24	-1.27	0.204
		q2	-0.66	0.81	-0.82	0.414	1.28	0.49	**2.62**	0.009	0.46	0.25	1.85	0.065	-0.27	0.24	-1.16	0.247
Beech Fruit Body	2012	q0	0.85	1.37	0.62	0.535	0.47	0.23	**2.09**	0.037	0.71	0.17	**4.22**	0.000	-0.16	0.17	-0.91	0.363
		q1	1.06	1.39	0.76	0.446	0.46	0.23	**2.00**	0.045	0.72	0.17	**4.26**	0.000	-0.18	0.18	-0.99	0.322
		q2	1.28	1.39	0.92	0.360	0.44	0.23	1.92	0.054	0.73	0.17	**4.35**	0.000	-0.20	0.18	-1.09	0.276
	2013	q0	-0.96	0.65	-1.48	0.139	0.74	0.23	**3.25**	0.001	0.40	0.12	**3.32**	0.001	-0.01	0.12	-0.11	0.912
		q1	-0.98	0.67	-1.45	0.148	0.74	0.23	**3.24**	0.001	0.40	0.12	**3.30**	0.001	-0.01	0.12	-0.10	0.918
		q2	-0.99	0.71	-1.40	0.161	0.74	0.23	**3.22**	0.001	0.39	0.12	**3.28**	0.001	-0.01	0.12	-0.09	0.927
		q0	-0.28	0.86	-0.33	0.744	0.83	0.33	**2.49**	0.013	0.36	0.12	**2.91**	0.004	0.04	0.12	0.31	0.760

	2015	q1	-0.30	0.89	-0.34	0.734	0.83	0.33	**2.49**	0.013	0.36	0.12	**2.92**	0.004	0.04	0.12	0.30	0.760
		q2	-0.34	0.94	-0.36	0.721	0.84	0.34	**2.50**	0.013	0.36	0.12	**2.92**	0.003	0.04	0.12	0.30	0.761
	2018	q0	-0.46	0.44	-1.05	0.295	0.79	0.22	**3.53**	0.000	0.34	0.12	**2.87**	0.004	0.06	0.12	0.54	0.587
		q1	-0.51	0.44	-1.15	0.250	0.80	0.22	**3.58**	0.000	0.34	0.12	**2.86**	0.004	0.07	0.12	0.58	0.563
		q2	-0.57	0.43	-1.30	0.192	0.81	0.22	**3.65**	0.000	0.34	0.12	**2.85**	0.004	0.07	0.12	0.63	0.526
	2021	q0	-1.19	0.68	-1.75	0.080	0.85	0.21	**3.94**	0.000	0.33	0.11	**2.91**	0.004	0.07	0.11	0.62	0.533
		q1	-1.28	0.68	-1.88	0.060	0.86	0.21	**4.03**	0.000	0.33	0.11	**2.92**	0.004	0.07	0.11	0.67	0.505
		q2	-1.40	0.68	**-2.07**	0.038	0.88	0.21	**4.17**	0.000	0.32	0.11	**2.93**	0.003	0.08	0.11	0.73	0.465
Fir Fruit Body	2012	q0																
		q1																
		q2																
	2013	q0	-0.20	0.72	-0.27	0.783	0.54	0.32	1.66	0.098	0.00	0.23	-0.02	0.984	0.24	0.20	1.20	0.228
		q1	-0.22	0.70	-0.31	0.758	0.54	0.32	1.67	0.096	0.00	0.23	-0.01	0.993	0.24	0.20	1.20	0.232
		q2	-0.24	0.67	-0.35	0.726	0.54	0.32	1.68	0.093	0.00	0.23	0.01	0.995	0.23	0.20	1.18	0.236
	2015	q0	0.76	0.96	0.78	0.433	1.13	0.40	**2.83**	0.005	0.52	0.27	1.91	0.056	-0.41	0.27	-1.53	0.125
		q1	0.76	1.00	0.76	0.445	1.13	0.40	**2.82**	0.005	0.52	0.27	1.90	0.057	-0.41	0.27	-1.52	0.127
		q2	0.77	1.05	0.73	0.463	1.13	0.40	**2.81**	0.005	0.52	0.27	1.89	0.059	-0.40	0.27	-1.51	0.130
	2018	q0	-1.61	0.64	**-2.51**	0.012	0.34	0.36	0.93	0.353	-0.18	0.23	-0.78	0.433	0.25	0.23	1.07	0.285
		q1	-1.66	0.66	**-2.51**	0.012	0.34	0.36	0.94	0.346	-0.18	0.23	-0.78	0.437	0.25	0.23	1.07	0.286
		q2	-1.73	0.70	**-2.50**	0.013	0.35	0.36	0.96	0.336	-0.17	0.23	-0.77	0.444	0.25	0.23	1.06	0.288

	2021	q0	-0.97	0.81	-1.19	0.232	1.31	0.43	**3.05**	0.002	0.50	0.25	**2.02**	0.044	-0.34	0.25	-1.35	0.178
		q1	-0.98	0.84	-1.17	0.243	1.31	0.43	**3.03**	0.002	0.50	0.25	**2.01**	0.044	-0.34	0.25	-1.34	0.179
		q2	-0.98	0.87	-1.12	0.261	1.30	0.43	**3.02**	0.003	0.50	0.25	**2.00**	0.045	-0.34	0.25	-1.34	0.180

Tab. S4 Annual linear mixed effect models (LMER) illustrating the influence of environmental factors on alpha species diversity (qD, estimated species richness). Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, t= t-value, p= p-value.

α – **LMER**			Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
			Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech Metabarcoding	2012	q0	0.21	0.16	1.34	0.206	-0.04	0.08	-0.55	0.590	0.03	0.09	0.34	0.740
		q1	0.17	0.13	1.34	0.201	-0.06	0.06	-1.03	0.318	0.07	0.06	1.04	0.313
		q2	0.08	0.10	0.81	0.431	-0.06	0.05	-1.13	0.277	0.05	0.05	0.86	0.401
	2013	q0	-0.32	0.08	**-3.80**	0.002	0.01	0.04	0.25	0.809	-0.04	0.05	-0.84	0.414
		q1	-0.20	0.07	**-2.90**	0.011	0.00	0.03	0.00	0.999	0.01	0.04	0.18	0.858
		q2	-0.14	0.07	-2.05	0.058	0.00	0.03	0.04	0.968	0.02	0.04	0.66	0.520
	2015	q0	0.43	0.12	**3.67**	0.002	0.03	0.06	0.45	0.656	-0.02	0.06	-0.27	0.788
		q1	0.27	0.12	**2.36**	0.031	0.03	0.06	0.40	0.692	-0.01	0.06	-0.15	0.882
		q2	0.07	0.12	0.61	0.551	0.04	0.07	0.62	0.547	-0.05	0.07	-0.71	0.487
	2018	q0	0.15	0.07	2.04	0.057	0.01	0.04	0.27	0.792	0.07	0.04	1.82	0.087
		q1	0.10	0.07	1.38	0.186	0.00	0.03	0.05	0.964	0.07	0.04	1.99	0.063
		q2	0.07	0.08	0.83	0.418	0.00	0.04	-0.07	0.947	0.06	0.04	1.50	0.152
	2021	q0	0.04	0.12	0.34	0.738	0.10	0.06	1.81	0.089	-0.01	0.06	-0.09	0.930
		q1	-0.03	0.09	-0.36	0.722	0.10	0.05	**2.16**	0.046	0.01	0.05	0.17	0.869
		q2	-0.07	0.08	-0.91	0.376	0.08	0.04	2.02	0.060	0.04	0.04	0.91	0.374

Fir Metabarcoding	2012	q0	0.30	0.15	2.04	0.058	0.06	0.09	0.65	0.524	-0.08	0.09	-0.90	0.380
		q1	0.20	0.13	1.58	0.133	0.06	0.08	0.76	0.456	0.00	0.08	-0.01	0.989
		q2	0.13	0.12	1.08	0.298	0.04	0.07	0.55	0.587	0.06	0.07	0.81	0.431
	2013	q0	-0.07	0.09	-0.81	0.431	-0.02	0.05	-0.42	0.683	0.06	0.05	1.22	0.239
		q1	0.00	0.10	0.02	0.987	-0.05	0.06	-0.81	0.431	0.11	0.06	1.76	0.097
		q2	0.03	0.11	0.25	0.804	-0.08	0.07	-1.11	0.283	0.14	0.07	2.08	0.054
	2015	q0	-0.11	0.16	-0.67	0.513	0.07	0.10	0.70	0.493	0.15	0.10	1.49	0.155
		q1	-0.13	0.14	-0.94	0.359	0.05	0.08	0.62	0.545	0.13	0.08	1.62	0.123
		q2	-0.10	0.13	-0.76	0.455	0.03	0.08	0.39	0.698	0.13	0.08	1.61	0.126
	2018	q0	0.12	0.10	1.19	0.251	-0.06	0.06	-1.05	0.309	0.01	0.06	0.24	0.811
		q1	0.13	0.12	1.08	0.295	-0.11	0.07	-1.62	0.126	0.04	0.07	0.56	0.586
		q2	0.13	0.13	1.04	0.316	-0.12	0.08	-1.45	0.166	0.06	0.08	0.74	0.478
	2021	q0	0.55	0.14	**3.96**	0.002	0.06	0.09	0.61	0.551	-0.03	0.11	-0.29	0.775
		q1	0.48	0.12	**3.99**	0.001	0.12	0.08	1.59	0.133	-0.10	0.08	-1.19	0.260
		q2	0.36	0.11	**3.28**	0.005	0.12	0.07	1.77	0.096	-0.07	0.07	-1.11	0.282
Beech Fruit Body	2012	q0	0.01	0.06	0.16	0.876	-0.05	0.03	-1.67	0.129	0.10	0.03	**3.64**	0.005
		q1	0.01	0.06	0.25	0.808	-0.05	0.03	-1.68	0.128	0.10	0.03	**3.75**	0.005
		q2	0.02	0.05	0.28	0.783	-0.04	0.03	-1.63	0.137	0.10	0.03	**3.78**	0.004
	2013	q0	0.10	0.06	1.62	0.129	0.01	0.03	0.43	0.673	0.02	0.04	0.43	0.672
		q1	0.10	0.06	1.63	0.127	0.01	0.03	0.41	0.692	0.02	0.03	0.45	0.661

		q2	0.09	0.06	1.64	0.124	0.01	0.03	0.36	0.722	0.02	0.03	0.47	0.646
	2015	q0	0.28	0.06	**4.44**	0.000	0.01	0.03	0.36	0.726	-0.01	0.03	-0.19	0.853
		q1	0.27	0.06	**4.47**	0.000	0.01	0.03	0.36	0.723	-0.01	0.03	-0.20	0.841
		q2	0.26	0.06	**4.50**	0.000	0.01	0.03	0.36	0.721	-0.01	0.03	-0.22	0.827
	2018	q0	0.05	0.12	0.44	0.663	-0.04	0.06	-0.65	0.526	0.05	0.06	0.80	0.438
		q1	0.06	0.12	0.48	0.636	-0.04	0.06	-0.68	0.509	0.05	0.06	0.81	0.432
		q2	0.06	0.12	0.54	0.595	-0.04	0.06	-0.72	0.482	0.05	0.06	0.83	0.419
	2021	q0	0.06	0.08	0.84	0.415	-0.03	0.04	-0.65	0.525	0.03	0.04	0.80	0.435
		q1	0.07	0.08	0.92	0.373	-0.03	0.04	-0.70	0.496	0.03	0.04	0.84	0.411
		q2	0.08	0.07	1.03	0.318	-0.03	0.04	-0.76	0.461	0.03	0.04	0.90	0.380
Fir Fruit Body	2012	q0												
		q1												
		q2												
	2013	q0	0.09	0.14	0.67	0.520	0.12	0.10	1.15	0.278	-0.08	0.09	-0.84	0.473
		q1	0.09	0.14	0.65	0.535	0.12	0.10	1.19	0.262	-0.09	0.10	-0.90	0.430
		q2	0.09	0.15	0.62	0.552	0.13	0.11	1.24	0.243	-0.10	0.10	-0.97	0.382
	2015	q0	-0.09	0.09	-0.97	0.349	-0.10	0.06	-1.69	0.111	0.06	0.07	0.80	0.441
		q1	-0.09	0.09	-1.00	0.334	-0.10	0.06	-1.71	0.107	0.06	0.07	0.83	0.424
		q2	-0.09	0.09	-1.04	0.314	-0.10	0.06	-1.74	0.101	0.06	0.06	0.88	0.397
		q0	-0.03	0.15	-0.21	0.840	0.02	0.10	0.25	0.805	-0.04	0.10	-0.40	0.706

	2018	q1	-0.03	0.15	-0.19	0.854	0.02	0.09	0.26	0.799	-0.04	0.10	-0.40	0.705
		q2	-0.02	0.14	-0.16	0.875	0.02	0.09	0.27	0.792	-0.04	0.10	-0.40	0.705
	2021	q0	0.17	0.13	1.29	0.218	0.08	0.08	1.07	0.304	-0.01	0.08	-0.15	0.879
		q1	0.16	0.13	1.30	0.214	0.08	0.07	1.08	0.298	-0.01	0.08	-0.14	0.889
		q2	0.16	0.12	1.32	0.208	0.08	0.07	1.09	0.293	-0.01	0.07	-0.12	0.903

Tab. S5 Annual structural equation models illustrating the influence of environmental factors and alpha species diversity (qD, estimated species richness) on deadwood density loss. Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, t= t-value, p= p-value.

α – **SEM**			Species diversity				Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
			Est	se	t	p	Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech Metabarcoding	2012	q0	0.09	0.08	1.13	0.260	0.16	0.05	**2.95**	0.003	0.08	0.02	**3.23**	0.001	0.00	0.03	0.17	0.865
		q1	0.12	0.11	1.12	0.265	0.17	0.05	**3.14**	0.002	0.08	0.02	**3.26**	0.001	0.00	0.03	0.18	0.859
		q2	0.14	0.13	1.07	0.284	0.17	0.05	**3.41**	0.001	0.08	0.03	**3.25**	0.001	0.01	0.03	0.24	0.809
	2013	q0	0.01	0.14	0.05	0.960	0.18	0.07	**2.72**	0.006	0.07	0.02	**3.19**	0.001	0.01	0.02	0.29	0.772
		q1	0.03	0.18	0.16	0.874	0.18	0.06	**3.06**	0.002	0.07	0.02	**3.18**	0.001	0.01	0.02	0.30	0.763
		q2	0.00	0.16	-0.02	0.985	0.17	0.05	**3.38**	0.001	0.07	0.02	**3.18**	0.001	0.01	0.02	0.29	0.774
	2015	q0	0.04	0.10	0.36	0.716	0.15	0.06	**2.52**	0.012	0.06	0.03	**2.27**	0.023	0.01	0.02	0.45	0.653
		q1	-0.07	0.10	-0.63	0.527	0.18	0.05	**3.55**	0.000	0.06	0.02	**2.41**	0.016	0.01	0.02	0.33	0.742
		q2	-0.11	0.09	-1.15	0.249	0.18	0.05	**3.96**	0.000	0.06	0.02	**2.47**	0.013	0.01	0.02	0.36	0.721
	2018	q0	0.02	0.15	0.12	0.907	0.17	0.05	**3.46**	0.001	0.07	0.02	**3.19**	0.001	0.01	0.03	0.22	0.823
		q1	0.01	0.15	0.07	0.941	0.17	0.05	**3.69**	0.000	0.07	0.02	**3.20**	0.001	0.01	0.03	0.23	0.816
		q2	-0.02	0.14	-0.17	0.864	0.18	0.05	**3.86**	0.000	0.07	0.02	**3.21**	0.001	0.01	0.02	0.33	0.745
	2021	q0	0.26	0.07	**3.50**	0.000	0.16	0.04	**4.54**	0.000	0.04	0.02	**2.33**	0.020	0.01	0.02	0.36	0.721
		q1	0.39	0.08	**4.81**	0.000	0.19	0.03	**5.95**	0.000	0.03	0.02	1.95	0.051	0.00	0.02	0.05	0.959

		q2	0.45	0.09	**5.05**	0.000	0.21	0.03	**6.72**	0.000	0.03	0.02	1.94	0.052	-0.01	0.02	-0.57	0.568
Fir Metabarcoding	2012	q0	-0.11	0.10	-1.09	0.274	0.18	0.06	**2.87**	0.004	-0.01	0.04	-0.23	0.815	0.05	0.05	1.13	0.259
		q1	-0.08	0.11	-0.77	0.441	0.16	0.06	**2.72**	0.006	-0.01	0.04	-0.13	0.898	0.05	0.05	1.10	0.269
		q2	-0.06	0.12	-0.48	0.630	0.15	0.06	**2.63**	0.008	-0.01	0.04	-0.14	0.888	0.05	0.05	1.08	0.280
	2013	q0	-0.25	0.15	-1.68	0.094	0.13	0.05	**2.39**	0.017	-0.01	0.04	-0.27	0.785	0.06	0.05	1.32	0.188
		q1	-0.13	0.14	-0.93	0.354	0.15	0.06	**2.65**	0.008	-0.01	0.04	-0.31	0.757	0.06	0.05	1.22	0.221
		q2	-0.07	0.12	-0.57	0.567	0.15	0.06	**2.64**	0.008	-0.01	0.04	-0.29	0.769	0.06	0.05	1.14	0.255
	2015	q0	-0.08	0.08	-1.06	0.290	0.13	0.05	**2.47**	0.014	0.00	0.04	0.03	0.975	0.05	0.05	1.10	0.270
		q1	-0.17	0.09	**-1.98**	0.048	0.12	0.05	**2.33**	0.020	0.01	0.04	0.15	0.878	0.06	0.04	1.37	0.172
		q2	-0.21	0.09	**-2.35**	0.019	0.12	0.05	**2.43**	0.015	0.00	0.04	-0.02	0.985	0.07	0.04	1.61	0.108
	2018	q0	0.12	0.14	0.85	0.395	0.12	0.06	**2.14**	0.032	0.01	0.04	0.13	0.898	0.03	0.05	0.70	0.485
		q1	0.13	0.12	1.07	0.285	0.12	0.06	**2.15**	0.032	0.01	0.04	0.30	0.767	0.03	0.05	0.62	0.537
		q2	0.11	0.10	1.09	0.275	0.13	0.06	**2.20**	0.028	0.01	0.04	0.19	0.853	0.04	0.05	0.72	0.471
	2021	q0	-0.13	0.09	-1.44	0.149	0.21	0.07	**2.99**	0.003	-0.01	0.04	-0.14	0.890	0.05	0.05	1.17	0.243
		q1	-0.13	0.11	-1.17	0.242	0.21	0.07	**2.75**	0.006	0.00	0.04	0.12	0.905	0.04	0.05	0.89	0.373
		q2	-0.10	0.12	-0.83	0.408	0.18	0.07	**2.56**	0.011	0.01	0.04	0.12	0.901	0.04	0.05	0.83	0.405
	2012	q0	-0.01	0.23	-0.02	0.982	0.09	0.04	**2.10**	0.036	0.13	0.02	**5.57**	0.000	-0.01	0.03	-0.36	0.716
		q1	0.06	0.24	0.24	0.807	0.09	0.04	**2.08**	0.037	0.13	0.02	**5.70**	0.000	-0.02	0.03	-0.57	0.572
		q2	0.13	0.24	0.55	0.583	0.09	0.04	**2.07**	0.038	0.13	0.02	**5.92**	0.000	-0.02	0.03	-0.81	0.420
		q0	-0.24	0.13	-1.88	0.061	0.17	0.04	**3.93**	0.000	0.08	0.02	**3.77**	0.000	0.00	0.02	-0.10	0.916

Beech Fruit Body	2013	q1	-0.24	0.13	-1.84	0.066	0.17	0.04	**3.92**	0.000	0.08	0.02	**3.75**	0.000	0.00	0.02	-0.10	0.924
		q2	-0.25	0.14	-1.78	0.075	0.17	0.04	**3.90**	0.000	0.08	0.02	**3.72**	0.000	0.00	0.02	-0.08	0.934
	2015	q0	-0.05	0.18	-0.28	0.783	0.19	0.07	**2.81**	0.005	0.07	0.02	**3.22**	0.001	0.01	0.02	0.29	0.773
		q1	-0.05	0.18	-0.29	0.772	0.19	0.07	**2.81**	0.005	0.07	0.02	**3.22**	0.001	0.01	0.02	0.29	0.774
		q2	-0.06	0.19	-0.31	0.757	0.19	0.07	**2.82**	0.005	0.07	0.02	**3.23**	0.001	0.01	0.02	0.29	0.775
	2018	q0	-0.13	0.10	-1.37	0.170	0.19	0.04	**4.24**	0.000	0.07	0.02	**2.97**	0.003	0.02	0.02	0.69	0.488
		q1	-0.14	0.10	-1.49	0.136	0.19	0.04	**4.29**	0.000	0.07	0.02	**2.96**	0.003	0.02	0.02	0.73	0.463
		q2	-0.15	0.09	-1.66	0.096	0.19	0.04	**4.38**	0.000	0.06	0.02	**2.94**	0.003	0.02	0.02	0.79	0.428
	2021	q0	-0.22	0.13	-1.69	0.091	0.19	0.04	**4.39**	0.000	0.07	0.02	**3.13**	0.002	0.01	0.02	0.58	0.561
		q1	-0.24	0.13	-1.84	0.066	0.19	0.04	**4.48**	0.000	0.07	0.02	**3.12**	0.002	0.01	0.02	0.63	0.531
		q2	-0.27	0.13	**-2.04**	0.041	0.20	0.04	**4.61**	0.000	0.06	0.02	**3.11**	0.002	0.02	0.02	0.69	0.488
Fir Fruit Body	2012	q0																
		q1																
		q2																
	2013	q0	0.03	0.12	0.25	0.805	0.09	0.05	1.68	0.094	-0.06	0.05	-1.22	0.222	0.13	0.05	**2.62**	0.009
		q1	0.03	0.11	0.23	0.819	0.09	0.05	1.69	0.091	-0.06	0.05	-1.21	0.226	0.13	0.05	**2.60**	0.009
		q2	0.02	0.11	0.21	0.835	0.09	0.05	1.71	0.088	-0.06	0.05	-1.20	0.231	0.13	0.05	**2.58**	0.010
	2015	q0	0.10	0.15	0.65	0.513	0.17	0.06	**2.80**	0.005	0.01	0.04	0.26	0.793	0.03	0.05	0.52	0.605
		q1	0.10	0.16	0.63	0.529	0.17	0.06	**2.79**	0.005	0.01	0.04	0.26	0.799	0.03	0.05	0.52	0.606
		q2	0.10	0.16	0.59	0.554	0.17	0.06	**2.78**	0.005	0.01	0.04	0.25	0.805	0.03	0.05	0.51	0.607
		q0	-0.30	0.11	**-2.70**	0.007	0.07	0.07	1.03	0.304	-0.05	0.06	-0.90	0.368	0.08	0.07	1.14	0.254

	2018	q1	-0.31	0.12	**-2.69**	0.007	0.07	0.07	1.04	0.299	-0.05	0.06	-0.90	0.370	0.08	0.07	1.14	0.254
		q2	-0.33	0.12	**-2.68**	0.007	0.08	0.07	1.06	0.290	-0.05	0.06	-0.89	0.373	0.08	0.07	1.14	0.254
	2021	q0	-0.30	0.14	**-2.11**	0.035	0.27	0.07	**3.83**	0.000	0.10	0.06	1.79	0.073	-0.09	0.07	-1.25	0.211
		q1	-0.31	0.15	**-2.06**	0.039	0.27	0.07	**3.80**	0.000	0.10	0.06	1.76	0.078	-0.08	0.07	-1.22	0.221
		q2	-0.31	0.16	**-2.00**	0.045	0.27	0.07	**3.75**	0.000	0.10	0.06	1.72	0.085	-0.08	0.07	-1.18	0.236

Influence of environmental factors on alpha species diversity (qD, estimated species richness).

α – **SEM**			Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
			Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech Metabarcoding	2012	q0	0.28	0.15	1.93	0.053	-0.05	0.07	-0.63	0.527	0.08	0.08	1.05	0.293
		q1	0.16	0.11	1.54	0.123	-0.04	0.05	-0.86	0.388	0.06	0.05	1.03	0.304
		q2	0.08	0.09	0.92	0.358	-0.04	0.04	-0.95	0.342	0.04	0.04	0.81	0.420
	2013	q0	-0.34	0.07	**-4.79**	0.000	0.01	0.03	0.42	0.676	-0.05	0.04	-1.33	0.183
		q1	-0.22	0.06	**-3.92**	0.000	0.01	0.03	0.40	0.688	-0.01	0.03	-0.47	0.640
		q2	-0.15	0.06	**-2.59**	0.010	0.02	0.03	0.54	0.589	0.00	0.03	-0.03	0.977
	2015	q0	0.42	0.10	**3.99**	0.000	0.03	0.06	0.54	0.589	-0.03	0.05	-0.48	0.629
		q1	0.25	0.10	**2.54**	0.011	0.03	0.05	0.55	0.581	-0.03	0.05	-0.60	0.550
		q2	0.10	0.11	0.90	0.369	0.02	0.06	0.31	0.760	-0.01	0.06	-0.26	0.792
	2018	q0	0.14	0.07	**2.18**	0.029	0.01	0.03	0.37	0.711	0.06	0.03	1.82	0.069
		q1	0.09	0.06	1.45	0.147	0.00	0.03	0.12	0.907	0.07	0.03	**2.01**	0.044
		q2	0.06	0.07	0.83	0.405	0.00	0.03	0.00	0.999	0.05	0.04	1.47	0.141
	2021	q0	0.05	0.10	0.43	0.665	0.10	0.05	1.96	0.050	0.00	0.05	0.01	0.995
		q1	-0.03	0.08	-0.31	0.758	0.10	0.04	**2.34**	0.019	0.02	0.04	0.35	0.728
		q2	-0.07	0.07	-0.98	0.325	0.08	0.04	**2.35**	0.019	0.04	0.04	0.92	0.359
	2012	q0	0.28	0.13	**2.22**	0.026	-0.02	0.09	-0.18	0.855	0.04	0.11	0.40	0.691
		q1	0.19	0.11	1.70	0.090	0.03	0.08	0.33	0.738	0.05	0.10	0.53	0.599

Fir Metabarcoding		q2	0.12	0.11	1.17	0.241	0.03	0.08	0.41	0.684	0.07	0.09	0.78	0.437
	2013	q0	-0.07	0.08	-0.86	0.390	-0.01	0.06	-0.21	0.837	0.05	0.07	0.69	0.493
		q1	0.00	0.09	0.05	0.957	-0.04	0.06	-0.60	0.550	0.09	0.08	1.13	0.260
		q2	0.03	0.10	0.32	0.752	-0.06	0.07	-0.89	0.375	0.12	0.09	1.38	0.167
	2015	q0	-0.10	0.15	-0.66	0.511	0.11	0.11	1.03	0.301	0.08	0.13	0.64	0.525
		q1	-0.12	0.12	-0.98	0.328	0.08	0.09	0.87	0.384	0.09	0.11	0.84	0.398
		q2	-0.10	0.12	-0.83	0.404	0.04	0.09	0.40	0.686	0.12	0.10	1.17	0.241
	2018	q0	0.10	0.09	1.16	0.248	-0.11	0.06	-1.80	0.073	0.09	0.08	1.24	0.217
		q1	0.11	0.10	1.04	0.297	-0.16	0.07	**-2.25**	0.024	0.12	0.09	1.35	0.176
		q2	0.11	0.12	0.90	0.368	-0.14	0.08	-1.65	0.098	0.10	0.10	0.95	0.340
	2021	q0	0.52	0.13	**3.94**	0.000	0.02	0.09	0.17	0.865	0.04	0.12	0.35	0.727
		q1	0.46	0.11	**4.20**	0.000	0.09	0.08	1.20	0.231	-0.05	0.10	-0.55	0.586
		q2	0.37	0.10	**3.66**	0.000	0.12	0.07	1.73	0.084	-0.08	0.09	-0.94	0.350
Beech Fruit Body	2012	q0	0.00	0.05	0.08	0.937	-0.05	0.02	-1.94	0.052	0.10	0.02	**4.39**	0.000
		q1	0.01	0.05	0.21	0.833	-0.05	0.02	-1.96	0.050	0.10	0.02	**4.51**	0.000
		q2	0.01	0.05	0.28	0.777	-0.04	0.02	-1.92	0.055	0.10	0.02	**4.52**	0.000
	2013	q0	0.01	0.08	0.18	0.854	0.04	0.04	1.08	0.281	-0.03	0.04	-0.80	0.424
		q1	0.01	0.08	0.18	0.857	0.04	0.04	1.06	0.290	-0.03	0.04	-0.79	0.429
		q2	0.01	0.07	0.17	0.862	0.04	0.03	1.02	0.305	-0.03	0.04	-0.78	0.435
	2015	q0	0.28	0.06	**5.11**	0.000	0.01	0.03	0.30	0.764	0.00	0.03	0.02	0.985
		q1	0.28	0.05	**5.13**	0.000	0.01	0.03	0.31	0.760	0.00	0.03	0.00	0.998

		q2	0.26	0.05	**5.17**	0.000	0.01	0.03	0.31	0.757	0.00	0.03	-0.03	0.979
	2018	q0	0.08	0.10	0.82	0.411	-0.05	0.05	-1.00	0.317	0.07	0.05	1.42	0.154
		q1	0.08	0.10	0.86	0.388	-0.05	0.05	-1.03	0.301	0.07	0.05	1.44	0.151
		q2	0.09	0.10	0.92	0.357	-0.05	0.05	-1.08	0.280	0.08	0.05	1.45	0.147
	2021	q0	0.06	0.07	0.87	0.384	-0.02	0.03	-0.68	0.499	0.03	0.04	0.77	0.442
		q1	0.07	0.07	0.96	0.337	-0.02	0.03	-0.73	0.466	0.03	0.04	0.82	0.414
		q2	0.07	0.07	1.08	0.278	-0.03	0.03	-0.80	0.426	0.03	0.04	0.88	0.378
Fir Fruit Body	2012	q0												
		q1												
		q2												
	2013	q0	0.11	0.12	0.96	0.336	0.17	0.09	1.75	0.080	-0.16	0.11	-1.50	0.133
		q1	0.11	0.12	0.90	0.367	0.17	0.10	1.78	0.075	-0.17	0.11	-1.56	0.119
		q2	0.10	0.12	0.83	0.404	0.18	0.10	1.83	0.068	-0.18	0.11	-1.64	0.100
	2015	q0	-0.10	0.08	-1.19	0.232	-0.08	0.06	-1.34	0.180	0.02	0.08	0.28	0.783
		q1	-0.10	0.08	-1.22	0.223	-0.08	0.06	-1.35	0.178	0.02	0.08	0.29	0.774
		q2	-0.10	0.08	-1.25	0.211	-0.08	0.06	-1.37	0.172	0.02	0.07	0.31	0.755
	2018	q0	0.01	0.15	0.09	0.930	0.08	0.12	0.66	0.507	-0.12	0.15	-0.81	0.416
		q1	0.02	0.15	0.11	0.914	0.08	0.11	0.67	0.503	-0.12	0.14	-0.81	0.416
		q2	0.02	0.14	0.14	0.890	0.07	0.11	0.68	0.497	-0.11	0.14	-0.81	0.416
		q0	0.27	0.10	**2.87**	0.004	0.24	0.07	**3.34**	0.001	-0.26	0.09	**-2.81**	0.005

	2021	q1	0.27	0.09	**2.89**	0.004	0.23	0.07	**3.34**	0.001	-0.25	0.09	**-2.79**	0.005
		q2	0.26	0.09	**2.91**	0.004	0.22	0.07	**3.36**	0.001	-0.24	0.09	**-2.78**	0.005

Tab. S6 Annual beta regression model illustrating the influence of environmental factors and beta species diversity (community composition) on deadwood density loss. Community composition was represented by vector predictors using the species scores from the first two axes (Ord1, Ord2) of the Principal Coordinates Analyses (see Method section). Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, z= z-value, p= p-value.

β – beta regression model			Species diversity								Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
			Ord1				Ord2															
			Est	se	z	p	Est	se	z	p	Est	se	z	p	Est	se	z	p	Est	se	z	p
Beech Metabarcoding	2012	q0	1.24	0.86	1.44	0.149	0.34	0.66	0.51	0.609	0.49	0.33	1.46	0.145	0.35	0.13	**2.75**	0.006	0.08	0.13	0.60	0.551
		q1	0.54	0.36	1.48	0.140	-0.20	0.35	-0.56	0.573	0.61	0.28	**2.22**	0.027	0.32	0.13	**2.46**	0.014	0.06	0.13	0.51	0.608
		q2	0.13	0.10	1.32	0.185	-0.08	0.11	-0.74	0.457	0.95	0.28	**3.34**	0.001	0.34	0.13	**2.60**	0.009	0.10	0.13	0.79	0.432
	2013	q0	4.72	1.50	**3.14**	0.002	0.63	0.65	0.98	0.329	2.63	0.61	**4.28**	0.000	0.32	0.10	**3.38**	0.001	0.11	0.10	1.03	0.303
		q1	-0.07	0.47	-0.16	0.874	-0.46	0.60	-0.77	0.440	0.68	0.25	**2.79**	0.005	0.35	0.12	**2.90**	0.004	0.04	0.12	0.31	0.755
		q2	-0.17	0.14	-1.22	0.222	0.20	0.15	1.36	0.175	0.69	0.22	**3.16**	0.002	0.43	0.13	**3.42**	0.001	0.01	0.11	0.10	0.922
	2015	q0	-0.40	0.76	-0.52	0.600	0.22	0.83	0.27	0.787	0.65	0.27	**2.39**	0.017	0.22	0.13	1.68	0.094	0.07	0.12	0.64	0.522
		q1	0.38	0.36	1.06	0.289	-0.05	0.48	-0.11	0.910	0.60	0.23	**2.57**	0.010	0.22	0.13	1.72	0.086	0.07	0.12	0.63	0.529
		q2	0.09	0.11	0.82	0.411	-0.17	0.12	-1.42	0.157	0.66	0.21	**3.13**	0.002	0.28	0.12	**2.31**	0.021	-0.01	0.12	-0.13	0.898
	2018	q0	-1.46	1.37	-1.06	0.288	-0.39	0.70	-0.56	0.578	1.40	0.66	**2.13**	0.033	0.31	0.12	**2.67**	0.008	0.09	0.12	0.71	0.476
		q1	-0.76	0.63	-1.19	0.233	-0.62	0.59	-1.06	0.288	1.22	0.42	**2.90**	0.004	0.35	0.12	**2.97**	0.003	0.08	0.12	0.66	0.511
		q2	-0.27	0.14	**-2.03**	0.043	0.14	0.14	0.97	0.330	0.68	0.21	**3.24**	0.001	0.39	0.11	**3.64**	0.000	0.01	0.11	0.10	0.920
	2021	q0	0.57	2.39	0.24	0.813	0.29	0.86	0.34	0.731	0.54	1.01	0.54	0.592	0.33	0.13	**2.64**	0.008	0.04	0.12	0.32	0.746
		q1	-0.23	0.61	-0.38	0.702	1.35	0.78	1.73	0.084	0.26	0.47	0.55	0.579	0.31	0.11	**2.85**	0.004	0.00	0.11	0.04	0.972
		q2	0.22	0.14	1.60	0.110	-0.13	0.16	-0.84	0.400	0.83	0.22	**3.75**	0.000	0.28	0.12	**2.26**	0.024	0.08	0.11	0.67	0.504
		q0	-0.62	1.00	-0.62	0.534	-2.79	1.46	-1.92	0.055	1.58	0.55	**2.89**	0.004	0.39	0.25	1.61	0.108	-0.21	0.23	-0.89	0.375

Fir Metabarcoding	2012	q1	0.76	0.62	1.22	0.222	-0.70	0.65	-1.07	0.283	1.19	0.41	**2.92**	0.004	0.45	0.24	1.85	0.064	-0.39	0.26	-1.49	0.137
		q2	0.15	0.25	0.58	0.561	0.00	0.26	-0.02	0.988	1.01	0.39	**2.62**	0.009	0.40	0.26	1.57	0.116	-0.22	0.24	-0.92	0.356
	2013	q0	1.76	2.44	0.72	0.470	1.93	1.22	1.58	0.114	0.36	0.87	0.42	0.678	0.41	0.24	1.71	0.088	-0.26	0.24	-1.09	0.277
		q1	-0.73	1.15	-0.64	0.524	-0.24	1.20	-0.20	0.842	1.26	0.63	**2.00**	0.046	0.32	0.24	1.33	0.183	-0.20	0.24	-0.84	0.403
		q2	0.04	0.23	0.18	0.857	0.10	0.21	0.50	0.618	1.00	0.39	**2.55**	0.011	0.35	0.25	1.40	0.161	-0.22	0.24	-0.92	0.357
	2015	q0	-1.02	0.95	-1.08	0.279	-1.39	1.19	-1.17	0.242	1.05	0.38	**2.79**	0.005	0.26	0.23	1.14	0.252	-0.11	0.23	-0.45	0.650
		q1	0.04	0.52	0.07	0.943	-1.13	0.73	-1.56	0.120	0.97	0.37	**2.66**	0.008	0.27	0.23	1.22	0.224	-0.07	0.24	-0.30	0.768
		q2	-0.13	0.18	-0.72	0.469	-0.13	0.17	-0.77	0.439	1.00	0.39	**2.57**	0.010	0.38	0.23	1.63	0.102	-0.33	0.25	-1.34	0.181
	2018	q0	1.12	1.60	0.70	0.484	-0.72	1.49	-0.48	0.632	0.47	0.73	0.65	0.518	0.41	0.27	1.51	0.132	-0.24	0.25	-0.97	0.331
		q1	0.33	0.89	0.37	0.714	-0.22	0.82	-0.27	0.790	0.88	0.56	1.58	0.115	0.40	0.24	1.68	0.092	-0.26	0.23	-1.10	0.271
		q2	0.11	0.23	0.51	0.614	-0.48	0.26	-1.82	0.068	0.69	0.38	1.84	0.066	0.32	0.24	1.32	0.186	-0.01	0.24	-0.02	0.983
	2021	q0	2.68	1.87	1.44	0.151	0.39	1.20	0.32	0.748	0.02	0.80	0.03	0.977	0.32	0.24	1.34	0.181	-0.21	0.23	-0.89	0.376
		q1	0.06	0.73	0.09	0.931	-0.60	0.78	-0.76	0.445	0.82	0.50	1.65	0.100	0.34	0.25	1.35	0.176	-0.22	0.24	-0.93	0.353
		q2	-0.18	0.24	-0.74	0.460	-0.33	0.26	-1.29	0.198	0.91	0.37	**2.44**	0.015	0.23	0.25	0.94	0.347	-0.03	0.25	-0.11	0.912
Beech Fruit Body	2012	q0	-0.40	0.67	-0.60	0.550	-0.29	0.48	-0.60	0.549	0.26	0.48	0.53	0.594	0.65	0.16	**4.19**	0.000	-0.05	0.11	-0.47	0.637
		q1	-0.29	0.55	-0.53	0.595	0.61	0.66	0.93	0.353	0.34	0.36	0.93	0.355	0.65	0.14	**4.58**	0.000	0.00	0.14	0.02	0.982
		q2	-0.19	0.11	-1.77	0.076	0.05	0.12	0.44	0.656	0.48	0.22	**2.19**	0.028	0.62	0.15	**4.16**	0.000	-0.01	0.10	-0.10	0.921
	2013	q0	0.40	0.53	0.76	0.450	0.36	0.44	0.81	0.416	0.42	0.42	0.99	0.321	0.33	0.13	**2.63**	0.009	0.02	0.12	0.16	0.875
		q1	0.32	0.62	0.52	0.605	0.24	0.50	0.47	0.640	0.53	0.41	1.27	0.203	0.33	0.13	**2.48**	0.013	0.02	0.12	0.15	0.881
		q2	0.02	0.18	0.12	0.901	0.13	0.17	0.78	0.434	0.75	0.25	**3.02**	0.003	0.34	0.13	**2.57**	0.010	0.04	0.13	0.29	0.773
	2015	q0	-0.12	0.61	-0.19	0.848	0.44	0.53	0.83	0.407	0.77	0.42	1.83	0.067	0.33	0.12	**2.70**	0.007	0.06	0.12	0.48	0.635
		q1	-0.39	0.66	-0.60	0.550	0.61	0.78	0.78	0.433	0.91	0.42	**2.14**	0.033	0.33	0.12	**2.68**	0.007	0.12	0.14	0.87	0.387
		q2	0.07	0.18	0.40	0.689	0.00	0.19	0.00	0.996	0.76	0.23	**3.26**	0.001	0.34	0.13	**2.71**	0.007	0.04	0.12	0.33	0.743
	2018	q0	0.96	0.67	1.43	0.153	0.63	0.50	1.25	0.210	0.22	0.42	0.51	0.610	0.36	0.12	**3.06**	0.002	-0.01	0.12	-0.12	0.905
		q1	0.51	0.85	0.60	0.547	-0.71	0.47	-1.49	0.135	0.53	0.47	1.13	0.258	0.37	0.12	**2.99**	0.003	0.02	0.13	0.18	0.860
		q2	-0.06	0.22	-0.25	0.800	0.31	0.23	1.36	0.175	0.76	0.22	**3.42**	0.001	0.37	0.12	**3.05**	0.002	0.07	0.12	0.61	0.541
		q0	0.61	0.36	1.72	0.086	0.78	0.35	**2.22**	0.026	0.84	0.20	**4.30**	0.000	0.35	0.11	**3.30**	0.001	0.18	0.12	1.50	0.132

	2021	q1	0.93	0.35	**2.68**	0.007	-0.67	0.36	-1.88	0.060	1.08	0.21	**5.16**	0.000	0.33	0.10	**3.30**	0.001	0.21	0.11	1.86	0.063
		q2	-0.18	0.20	-0.88	0.381	0.09	0.19	0.50	0.620	0.78	0.23	**3.42**	0.001	0.33	0.12	**2.72**	0.006	0.04	0.12	0.38	0.704
Fir Fruit Body	2012	q0																				
		q1																				
		q2																				
	2013	q0	-0.24	0.52	-0.47	0.641	-0.22	0.39	-0.57	0.569	0.35	0.48	0.72	0.472	-0.09	0.23	-0.38	0.702	0.31	0.21	1.48	0.139
		q1	-0.09	0.48	-0.18	0.857	-0.17	0.50	-0.34	0.730	0.51	0.47	1.09	0.277	-0.05	0.24	-0.21	0.833	0.28	0.21	1.33	0.183
		q2	0.24	0.23	1.04	0.296	-0.27	0.18	-1.56	0.119	0.59	0.30	1.95	0.052	0.14	0.23	0.61	0.540	0.13	0.20	0.67	0.504
	2015	q0	1.02	0.57	1.81	0.070	-0.37	0.72	-0.51	0.609	0.93	0.54	1.71	0.087	0.26	0.23	1.12	0.264	-0.04	0.25	-0.18	0.858
		q1	-0.34	0.67	-0.51	0.607	-0.98	0.64	-1.53	0.126	0.88	0.66	1.32	0.188	0.28	0.23	1.20	0.230	-0.07	0.24	-0.30	0.762
		q2	-0.20	0.21	-0.96	0.339	-0.02	0.19	-0.12	0.902	1.08	0.39	**2.77**	0.006	0.42	0.24	1.72	0.085	-0.40	0.26	-1.54	0.123
	2018	q0	1.76	0.59	**2.96**	0.003	-1.01	0.42	**-2.39**	0.017	-0.93	0.52	-1.76	0.078	-0.13	0.24	-0.53	0.596	0.51	0.29	1.74	0.082
		q1	1.18	0.47	**2.51**	0.012	-1.70	0.50	**-3.41**	0.001	-1.11	0.55	**-2.02**	0.043	-0.43	0.24	-1.76	0.078	0.76	0.31	**2.44**	0.015
		q2	-0.04	0.18	-0.24	0.809	-0.10	0.15	-0.66	0.510	0.43	0.45	0.94	0.349	-0.17	0.29	-0.60	0.548	0.29	0.28	1.01	0.313
	2021	q0	-0.85	0.63	-1.36	0.175	-0.13	0.64	-0.20	0.838	1.36	0.52	**2.63**	0.009	0.22	0.28	0.77	0.439	-0.17	0.26	-0.67	0.505
		q1	-0.84	0.61	-1.37	0.169	-0.12	0.57	-0.21	0.830	1.38	0.47	**2.91**	0.004	0.21	0.28	0.72	0.469	-0.16	0.26	-0.60	0.546
		q2	0.28	0.22	1.26	0.207	0.65	0.28	**2.31**	0.021	0.54	0.45	1.19	0.235	0.15	0.26	0.55	0.582	0.13	0.32	0.42	0.677

Tab. S7 Annual linear mixed effect models (LMER) illustrating the influence of environmental factors on beta species diversity (community composition). Community composition was represented by vector predictors using the species scores from the first two axes (Ord1, Ord2) of the Principal Coordinates Analyses (see Method section). Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, t= t-value, p= p-value.

β - **LMER**				Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
				Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech metabarcoding	2012	Ord1	q0	0.24	0.08	**3.11**	0.007	0.00	0.04	0.03	0.974	-0.02	0.04	-0.60	0.558
			q1	0.35	0.15	**2.30**	0.038	0.10	0.07	1.33	0.207	0.02	0.09	0.24	0.817
			q2	-0.37	0.67	-0.54	0.595	0.17	0.32	0.53	0.603	-0.24	0.35	-0.69	0.501
		Ord2	q0	0.11	0.10	1.12	0.281	0.00	0.05	0.01	0.990	0.03	0.05	0.66	0.517
			q1	-0.08	0.18	-0.45	0.660	0.03	0.09	0.32	0.753	0.06	0.09	0.60	0.561
			q2	1.27	0.60	2.10	0.053	0.00	0.29	0.02	0.987	0.14	0.31	0.46	0.649
	2013	Ord1	q0	-0.39	0.03	**-12.69**	0.000	0.00	0.01	0.25	0.807	-0.01	0.02	-0.47	0.644
			q1	0.06	0.12	0.48	0.639	-0.01	0.06	-0.12	0.904	0.04	0.06	0.68	0.507
			q2	-0.14	0.38	-0.36	0.726	0.17	0.18	0.93	0.365	-0.03	0.20	-0.18	0.863
		Ord2	q0	-0.05	0.06	-0.73	0.478	0.00	0.03	-0.01	0.989	-0.04	0.04	-1.14	0.270
			q1	-0.15	0.09	-1.65	0.116	0.02	0.04	0.53	0.603	0.01	0.05	0.17	0.870
			q2	0.25	0.33	0.74	0.468	-0.30	0.16	-1.81	0.088	0.14	0.18	0.74	0.468
	2015	Ord1	q0	-0.17	0.07	**-2.27**	0.037	-0.03	0.04	-0.85	0.410	0.03	0.04	0.80	0.433
			q1	0.24	0.15	1.62	0.124	0.07	0.08	0.85	0.408	-0.06	0.08	-0.76	0.456
			q2	-0.05	0.43	-0.12	0.907	0.12	0.24	0.50	0.626	0.07	0.24	0.29	0.777

		Ord2	q0	-0.10	0.06	-1.49	0.157	0.02	0.04	0.65	0.524	-0.03	0.03	-0.83	0.417
			q1	-0.04	0.11	-0.35	0.733	0.01	0.06	0.20	0.842	-0.06	0.06	-1.10	0.289
			q2	-0.28	0.42	-0.67	0.514	0.29	0.23	1.23	0.235	-0.36	0.22	-1.67	0.115
	2018	Ord1	q0	0.44	0.04	**10.84**	0.000	-0.01	0.02	-0.64	0.533	0.03	0.02	1.62	0.125
			q1	0.44	0.10	**4.57**	0.000	0.04	0.05	0.95	0.356	0.03	0.05	0.62	0.541
			q2	-0.14	0.37	-0.39	0.703	0.13	0.18	0.73	0.473	0.05	0.19	0.29	0.779
		Ord2	q0	-0.01	0.07	-0.13	0.896	-0.03	0.03	-0.77	0.454	0.02	0.04	0.51	0.615
			q1	0.21	0.11	2.03	0.058	-0.04	0.05	-0.80	0.434	0.03	0.05	0.60	0.556
			q2	0.34	0.34	1.00	0.331	-0.10	0.16	-0.62	0.544	0.32	0.18	1.79	0.092
	2021	Ord1	q0	0.40	0.03	**14.74**	0.000	0.02	0.01	1.39	0.183	-0.01	0.01	-0.46	0.648
			q1	-0.34	0.11	**-3.07**	0.008	0.02	0.05	0.43	0.673	0.00	0.06	-0.06	0.952
			q2	-0.13	0.40	-0.32	0.751	0.05	0.19	0.27	0.791	-0.19	0.20	-0.93	0.367
		Ord2	q0	-0.08	0.06	-1.24	0.235	0.03	0.03	0.91	0.378	-0.04	0.04	-1.03	0.320
			q1	0.32	0.09	**3.62**	0.002	0.02	0.04	0.51	0.617	0.02	0.05	0.46	0.648
			q2	0.27	0.34	0.79	0.440	-0.39	0.17	**-2.33**	0.033	0.10	0.19	0.55	0.590
Fir metabarcoding	2012	Ord1	q0	0.12	0.07	1.70	0.113	0.05	0.05	0.97	0.346	-0.11	0.06	-1.92	0.073
			q1	-0.16	0.12	-1.29	0.219	0.12	0.08	1.42	0.177	-0.13	0.10	-1.36	0.193
			q2	0.04	0.37	0.12	0.908	-0.14	0.23	-0.61	0.552	-0.15	0.25	-0.59	0.570
		Ord2	q0	0.23	0.06	**3.67**	0.003	0.04	0.04	0.92	0.372	-0.01	0.04	-0.16	0.873
			q1	0.09	0.14	0.65	0.525	0.14	0.08	1.65	0.119	-0.17	0.08	-2.07	0.055
			q2	-0.06	0.37	-0.15	0.882	0.33	0.22	1.49	0.156	-0.16	0.22	-0.70	0.494
		Ord1	q0	0.32	0.04	**8.66**	0.000	-0.02	0.02	-0.90	0.379	0.00	0.02	-0.04	0.969

	2013		q1	0.37	0.09	**4.22**	0.001	-0.05	0.05	-0.90	0.384	0.02	0.05	0.36	0.725
			q2	0.21	0.43	0.50	0.627	0.10	0.26	0.40	0.695	0.24	0.26	0.94	0.360
		Ord2	q0	0.02	0.08	0.28	0.784	-0.02	0.05	-0.38	0.712	0.04	0.05	0.74	0.478
			q1	0.11	0.09	1.25	0.230	0.01	0.05	0.16	0.877	-0.05	0.05	-1.01	0.325
			q2	0.14	0.44	0.31	0.760	0.32	0.27	1.20	0.246	-0.19	0.26	-0.73	0.479
	2015	Ord1	q0	0.02	0.09	0.19	0.854	-0.04	0.06	-0.71	0.484	0.07	0.05	1.34	0.197
			q1	0.09	0.16	0.55	0.588	0.01	0.10	0.11	0.914	0.01	0.10	0.07	0.947
			q2	0.59	0.50	1.19	0.251	0.15	0.31	0.48	0.639	-0.42	0.30	-1.42	0.173
		Ord2	q0	0.08	0.07	1.09	0.291	-0.01	0.04	-0.33	0.744	0.02	0.04	0.40	0.692
			q1	0.05	0.12	0.42	0.682	-0.06	0.07	-0.78	0.445	0.15	0.08	1.99	0.094
			q2	-0.02	0.51	-0.05	0.963	0.08	0.32	0.25	0.806	-0.31	0.33	-0.94	0.370
	2018	Ord1	q0	0.37	0.06	**5.85**	0.000	0.02	0.04	0.60	0.554	-0.04	0.04	-1.02	0.322
			q1	0.39	0.11	**3.52**	0.003	-0.01	0.07	-0.08	0.935	-0.03	0.06	-0.40	0.695
			q2	-0.06	0.40	-0.16	0.875	-0.28	0.24	-1.17	0.259	0.11	0.23	0.49	0.633
		Ord2	q0	-0.03	0.06	-0.51	0.619	0.11	0.04	**2.89**	0.011	-0.06	0.04	-1.50	0.153
			q1	0.17	0.12	1.42	0.175	0.05	0.07	0.67	0.515	0.01	0.07	0.14	0.891
			q2	-0.37	0.35	-1.05	0.308	0.02	0.21	0.11	0.910	0.36	0.21	1.75	0.100
	2021	Ord1	q0	0.37	0.05	**7.84**	0.000	0.04	0.03	1.35	0.197	-0.02	0.03	-0.75	0.466
			q1	-0.26	0.13	-1.97	0.067	0.14	0.08	1.75	0.100	-0.04	0.08	-0.48	0.637
			q2	-0.08	0.39	-0.20	0.848	0.21	0.23	0.90	0.379	-0.04	0.23	-0.16	0.876
		Ord2	q0	0.01	0.05	0.14	0.887	0.01	0.04	0.34	0.735	-0.04	0.04	-1.01	0.328
			q1	-0.25	0.12	-2.08	0.054	-0.06	0.07	-0.77	0.453	0.03	0.07	0.44	0.666

			q2	-0.05	0.36	-0.14	0.888	-0.36	0.22	-1.65	0.118	0.40	0.21	1.85	0.083
Beech fruit body	2012	Ord1	q0	-0.51	0.12	**-4.30**	0.002	-0.05	0.06	-0.88	0.404	-0.01	0.05	-0.11	0.914
			q1	-0.52	0.14	**-3.73**	0.005	-0.02	0.07	-0.24	0.815	-0.03	0.06	-0.42	0.682
			q2	0.15	0.60	0.25	0.812	-0.15	0.30	-0.50	0.631	0.09	0.28	0.34	0.742
		Ord2	q0	0.14	0.17	0.84	0.422	-0.03	0.08	-0.31	0.761	0.02	0.08	0.29	0.776
			q1	-0.03	0.12	-0.26	0.799	0.03	0.06	0.54	0.605	-0.16	0.06	**-2.80**	0.021
			q2	0.09	0.56	0.16	0.877	-0.28	0.29	-0.99	0.360	-0.07	0.26	-0.28	0.787
	2013	Ord1	q0	0.61	0.12	**4.93**	0.000	0.06	0.06	1.03	0.318	-0.01	0.06	-0.09	0.927
			q1	0.52	0.11	**4.89**	0.000	0.07	0.05	1.36	0.193	0.01	0.05	0.20	0.844
			q2	-0.21	0.35	-0.61	0.553	0.15	0.17	0.87	0.396	-0.23	0.18	-1.28	0.218
		Ord2	q0	0.17	0.15	1.17	0.260	-0.02	0.07	-0.24	0.815	0.01	0.08	0.19	0.853
			q1	0.12	0.13	0.91	0.375	0.01	0.06	0.22	0.825	0.01	0.06	0.11	0.915
			q2	-0.12	0.36	-0.34	0.739	0.16	0.17	0.90	0.383	-0.06	0.19	-0.35	0.733
	2015	Ord1	q0	0.57	0.09	**6.03**	0.000	0.01	0.05	0.20	0.841	0.07	0.05	1.45	0.166
			q1	0.52	0.09	**5.97**	0.000	-0.02	0.04	-0.44	0.662	0.07	0.05	1.46	0.163
			q2	-0.12	0.30	-0.41	0.687	0.12	0.15	0.78	0.446	-0.09	0.15	-0.57	0.575
		Ord2	q0	0.08	0.11	0.73	0.477	0.04	0.05	0.75	0.461	-0.05	0.06	-0.91	0.374
			q1	0.06	0.07	0.82	0.423	0.03	0.04	0.79	0.440	-0.12	0.04	**-3.01**	0.008
			q2	0.03	0.29	0.11	0.917	-0.02	0.15	-0.11	0.914	0.16	0.15	1.08	0.294
	2018	Ord1	q0	0.53	0.08	**6.95**	0.000	-0.04	0.04	-1.03	0.317	0.06	0.04	1.45	0.165
			q1	0.49	0.06	**7.83**	0.000	-0.04	0.03	-1.34	0.199	0.07	0.03	2.04	0.059
			q2	-0.09	0.24	-0.39	0.703	-0.06	0.12	-0.52	0.607	-0.05	0.12	-0.42	0.676

		Ord2	q0	0.03	0.10	0.28	0.781	0.05	0.05	0.88	0.393	-0.04	0.06	-0.75	0.463
			q1	0.03	0.11	0.30	0.770	0.00	0.06	0.07	0.942	0.04	0.06	0.67	0.511
			q2	-0.03	0.23	-0.11	0.912	-0.03	0.12	-0.26	0.801	-0.11	0.12	-0.90	0.381
	2021	Ord1	q0	0.02	0.11	0.23	0.824	0.00	0.06	0.04	0.967	-0.10	0.06	-1.60	0.129
			q1	-0.14	0.12	-1.12	0.279	0.02	0.06	0.25	0.804	-0.11	0.07	-1.64	0.119
			q2	0.15	0.29	0.53	0.600	-0.09	0.14	-0.59	0.562	-0.02	0.15	-0.14	0.894
		Ord2	q0	-0.05	0.14	-0.37	0.719	-0.02	0.07	-0.24	0.811	-0.06	0.07	-0.84	0.413
			q1	0.18	0.13	1.37	0.191	-0.01	0.07	-0.15	0.879	0.05	0.07	0.77	0.454
			q2	-0.01	0.28	-0.04	0.971	0.06	0.14	0.44	0.666	-0.15	0.15	-1.03	0.320
Fir fruit body	2012	Ord1	q0												
			q1												
			q2												
		Ord2	q0												
			q1												
			q2												
	2013	Ord1	q0	-0.69	0.19	**-3.64**	0.005	-0.09	0.13	-0.65	0.530	0.04	0.11	0.35	0.730
			q1	-0.56	0.22	**-2.52**	0.030	-0.16	0.15	-1.03	0.326	0.11	0.13	0.81	0.436
			q2	0.31	0.43	0.71	0.497	-0.47	0.30	-1.56	0.149	0.34	0.26	1.31	0.219
		Ord2	q0	-0.06	0.26	-0.22	0.831	-0.13	0.18	-0.72	0.488	0.19	0.16	1.24	0.242
			q1	0.29	0.21	1.39	0.207	0.01	0.15	0.04	0.972	0.04	0.14	0.26	0.809
			q2	0.46	0.45	1.01	0.338	0.20	0.34	0.60	0.563	-0.27	0.34	-0.79	0.448
		Ord1	q0	0.31	0.16	1.93	0.072	0.07	0.10	0.71	0.489	-0.19	0.10	-1.91	0.103

	2015		q1	0.50	0.15	**3.33**	0.004	-0.11	0.09	-1.23	0.235	0.11	0.09	1.13	0.276
			q2	0.13	0.46	0.28	0.782	0.01	0.28	0.04	0.968	-0.41	0.29	-1.44	0.169
		Ord2	q0	0.39	0.13	**3.08**	0.007	-0.11	0.08	-1.36	0.193	0.04	0.08	0.56	0.581
			q1	-0.42	0.16	**-2.69**	0.016	-0.06	0.10	-0.65	0.524	0.16	0.10	1.64	0.121
			q2	0.14	0.50	0.28	0.785	-0.08	0.31	-0.25	0.803	-0.09	0.31	-0.27	0.788
	2018	Ord1	q0	0.61	0.16	**3.76**	0.002	-0.08	0.11	-0.78	0.454	-0.02	0.12	-0.12	0.905
			q1	0.71	0.19	**3.66**	0.003	-0.05	0.12	-0.42	0.680	-0.03	0.13	-0.23	0.824
			q2	0.57	0.67	0.85	0.410	0.45	0.42	1.07	0.303	0.22	0.44	0.51	0.621
		Ord2	q0	-0.21	0.23	-0.91	0.379	0.00	0.16	0.03	0.975	0.06	0.19	0.31	0.762
			q1	-0.36	0.20	-1.82	0.092	-0.09	0.14	-0.66	0.523	0.14	0.17	0.84	0.417
			q2	0.24	0.81	0.29	0.774	-0.26	0.51	-0.51	0.616	0.04	0.53	0.08	0.938
	2021	Ord1	q0	0.31	0.19	1.68	0.115	-0.23	0.11	-2.06	0.058	0.12	0.11	1.07	0.302
			q1	0.30	0.18	1.64	0.123	-0.25	0.11	**-2.38**	0.032	0.14	0.11	1.29	0.218
			q2	0.22	0.48	0.47	0.647	-0.06	0.29	-0.22	0.833	-0.12	0.32	-0.39	0.719
		Ord2	q0	-0.25	0.18	-1.39	0.186	0.08	0.11	0.72	0.484	0.01	0.11	0.07	0.942
			q1	-0.14	0.20	-0.73	0.477	0.07	0.12	0.62	0.548	0.06	0.12	0.51	0.619
			q2	1.27	0.31	**4.11**	0.002	0.77	0.22	**3.43**	0.004	-1.19	0.29	**-4.08**	0.001

Tab. S8 Annual structural equation models illustrating the influence of environmental factors and beta species diversity (community composition) on deadwood density loss. Community composition was represented by vector predictors using the species scores from the first two axes (Ord1, Ord2) of the Principal Coordinates Analyses (see Method section). Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, t= t-value, p= p-value.

β – **SEM**			Species diversity								Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
			Ord1				Ord2															
			Est	se	t	p	Est	se	t	p	Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech Metabarcoding	2012	q0	0.30	0.17	1.80	0.072	0.10	0.13	0.75	0.453	0.10	0.06	1.66	0.096	0.07	0.02	**3.04**	0.002	0.02	0.03	0.70	0.482
		q1	0.17	0.09	1.98	0.048	-0.04	0.07	-0.65	0.514	0.12	0.05	**2.27**	0.023	0.06	0.03	**2.19**	0.028	0.02	0.02	0.69	0.489
		q2	0.02	0.02	1.34	0.182	-0.03	0.02	-1.44	0.149	0.23	0.05	**4.29**	0.000	0.07	0.02	**3.00**	0.003	0.02	0.03	0.89	0.372
	2013	q0	1.23	0.28	**4.40**	0.000	0.22	0.11	1.90	0.058	0.66	0.12	**5.75**	0.000	0.06	0.02	**3.92**	0.000	0.03	0.02	1.64	0.101
		q1	-0.03	0.09	-0.36	0.717	-0.09	0.12	-0.79	0.428	0.16	0.05	**3.39**	0.001	0.07	0.02	**3.32**	0.001	0.01	0.02	0.38	0.704
		q2	-0.03	0.03	-1.22	0.224	0.04	0.03	1.38	0.169	0.16	0.04	**3.66**	0.000	0.09	0.02	**3.86**	0.000	0.00	0.02	-0.01	0.991
	2015	q0	-0.14	0.15	-0.93	0.351	0.05	0.18	0.30	0.764	0.15	0.06	**2.70**	0.007	0.05	0.03	**2.04**	0.042	0.02	0.02	0.63	0.532
		q1	0.11	0.07	1.57	0.117	-0.01	0.09	-0.15	0.877	0.14	0.05	**2.96**	0.003	0.05	0.02	**2.10**	0.036	0.01	0.02	0.61	0.545
		q2	0.03	0.02	1.34	0.181	-0.04	0.02	-1.80	0.072	0.15	0.04	**3.68**	0.000	0.07	0.02	**2.89**	0.004	-0.01	0.02	-0.47	0.639
	2018	q0	-0.29	0.26	-1.14	0.253	-0.15	0.15	-0.98	0.326	0.30	0.12	**2.53**	0.011	0.06	0.02	**2.94**	0.003	0.02	0.02	0.86	0.391
		q1	-0.20	0.11	-1.92	0.055	-0.18	0.10	-1.90	0.058	0.31	0.07	**4.61**	0.000	0.07	0.02	**3.33**	0.001	0.02	0.02	0.96	0.339
		q2	-0.06	0.03	**-2.30**	0.022	0.04	0.03	1.55	0.122	0.15	0.04	**3.72**	0.000	0.08	0.02	**4.29**	0.000	-0.01	0.02	-0.25	0.802
	2021	q0	0.10	0.40	0.26	0.796	0.13	0.17	0.74	0.457	0.14	0.17	0.86	0.387	0.07	0.02	**2.85**	0.004	0.01	0.02	0.44	0.657
		q1	-0.03	0.08	-0.31	0.753	0.30	0.11	**2.84**	0.005	0.07	0.06	1.19	0.235	0.06	0.02	**3.29**	0.001	0.00	0.02	0.09	0.926
		q2	0.05	0.03	1.91	0.056	-0.01	0.03	-0.50	0.619	0.19	0.04	**4.41**	0.000	0.06	0.02	**2.61**	0.009	0.02	0.02	0.85	0.396
	2012	q0	0.15	0.18	0.85	0.393	-0.53	0.21	**-2.52**	0.012	0.24	0.07	**3.40**	0.001	-0.02	0.04	-0.45	0.655	0.10	0.05	1.93	0.054
		q1	0.19	0.12	1.60	0.109	-0.14	0.09	-1.50	0.133	0.18	0.05	**3.41**	0.001	-0.01	0.04	-0.35	0.729	0.06	0.05	1.10	0.272

Fir Metabarcoding		q2	0.04	0.04	0.96	0.337	-0.01	0.04	-0.32	0.749	0.14	0.06	**2.57**	0.010	0.00	0.04	-0.07	0.948	0.06	0.05	1.20	0.232
	2013	q0	0.37	0.37	1.02	0.309	0.24	0.17	1.38	0.168	0.02	0.13	0.14	0.888	0.00	0.04	-0.06	0.948	0.05	0.05	1.12	0.264
		q1	-0.12	0.16	-0.79	0.428	-0.06	0.16	-0.40	0.691	0.20	0.08	**2.41**	0.016	-0.01	0.04	-0.34	0.735	0.05	0.05	1.02	0.309
		q2	0.01	0.03	0.28	0.778	0.04	0.03	1.17	0.244	0.14	0.05	**2.57**	0.010	-0.01	0.04	-0.32	0.752	0.04	0.05	0.82	0.413
	2015	q0	-0.22	0.13	-1.63	0.103	-0.19	0.18	-1.07	0.285	0.16	0.05	**3.02**	0.003	-0.03	0.04	-0.73	0.467	0.08	0.05	1.63	0.103
		q1	-0.05	0.07	-0.71	0.478	-0.24	0.11	-2.10	0.035	0.15	0.05	**3.01**	0.003	-0.04	0.04	-1.05	0.292	0.11	0.05	2.12	0.034
		q2	-0.02	0.03	-0.57	0.567	-0.02	0.02	-0.61	0.539	0.15	0.06	**2.68**	0.007	-0.01	0.04	-0.19	0.850	0.04	0.05	0.80	0.422
	2018	q0	0.06	0.22	0.28	0.777	0.00	0.20	0.01	0.991	0.11	0.10	1.13	0.257	-0.01	0.05	-0.20	0.838	0.05	0.05	0.94	0.349
		q1	0.02	0.14	0.13	0.893	-0.14	0.12	-1.11	0.268	0.16	0.08	**2.02**	0.043	0.01	0.04	0.21	0.837	0.03	0.05	0.61	0.542
		q2	0.01	0.03	0.43	0.665	-0.05	0.04	-1.41	0.159	0.12	0.06	**2.02**	0.043	-0.01	0.04	-0.22	0.823	0.07	0.05	1.46	0.145
	2021	q0	0.36	0.31	1.17	0.243	0.21	0.18	1.19	0.234	0.01	0.12	0.09	0.932	-0.01	0.04	-0.37	0.713	0.05	0.05	1.06	0.290
		q1	-0.05	0.11	-0.48	0.629	-0.07	0.12	-0.59	0.557	0.11	0.07	1.67	0.095	0.00	0.05	-0.05	0.959	0.05	0.05	0.91	0.364
		q2	-0.02	0.03	-0.45	0.650	-0.05	0.04	-1.34	0.180	0.14	0.05	**2.57**	0.010	-0.03	0.04	-0.76	0.450	0.09	0.05	1.60	0.109
Beech Fruit Body	2012	q0	-0.05	0.10	-0.54	0.592	-0.12	0.07	-1.67	0.095	0.07	0.07	1.09	0.278	0.12	0.02	**6.70**	0.000	-0.01	0.02	-0.46	0.648
		q1	0.03	0.10	0.26	0.792	0.04	0.11	0.36	0.716	0.10	0.06	1.63	0.104	0.13	0.02	**6.15**	0.000	0.00	0.03	-0.16	0.873
		q2	-0.05	0.02	-3.27	0.001	0.00	0.02	-0.15	0.877	0.09	0.03	**2.86**	0.004	0.12	0.02	**7.65**	0.000	0.00	0.01	-0.35	0.729
	2013	q0	0.07	0.09	0.74	0.462	0.07	0.08	0.95	0.343	0.11	0.08	1.53	0.126	0.07	0.02	**2.99**	0.003	0.00	0.02	0.19	0.852
		q1	0.04	0.11	0.40	0.687	0.05	0.09	0.59	0.554	0.14	0.08	1.87	0.061	0.07	0.02	**2.85**	0.004	0.00	0.02	0.19	0.850
		q2	0.01	0.03	0.18	0.861	0.02	0.03	0.53	0.594	0.17	0.05	**3.60**	0.000	0.07	0.02	**2.91**	0.004	0.01	0.03	0.29	0.774
	2015	q0	-0.03	0.11	-0.23	0.820	0.11	0.10	1.10	0.269	0.18	0.08	**2.35**	0.019	0.07	0.02	**3.06**	0.002	0.01	0.02	0.57	0.566
		q1	-0.10	0.12	-0.80	0.422	0.14	0.14	0.99	0.320	0.21	0.08	**2.85**	0.004	0.07	0.02	**3.06**	0.002	0.03	0.03	0.98	0.326
		q2	0.02	0.04	0.60	0.545	0.01	0.04	0.15	0.879	0.18	0.04	**3.94**	0.000	0.07	0.02	**3.09**	0.002	0.01	0.02	0.28	0.778
	2018	q0	0.19	0.13	1.50	0.134	0.12	0.10	1.21	0.227	0.07	0.08	0.84	0.400	0.07	0.02	**3.37**	0.001	0.00	0.02	-0.01	0.995
		q1	0.06	0.16	0.38	0.707	-0.17	0.09	-1.87	0.061	0.15	0.09	1.67	0.095	0.08	0.02	**3.53**	0.000	0.01	0.02	0.26	0.796
		q2	-0.03	0.04	-0.68	0.496	0.07	0.04	1.48	0.139	0.17	0.04	**4.06**	0.000	0.07	0.02	**3.40**	0.001	0.01	0.02	0.49	0.621
	2021	q0	0.14	0.07	**2.02**	0.043	0.17	0.07	2.44	0.015	0.18	0.04	**4.89**	0.000	0.07	0.02	**3.66**	0.000	0.04	0.02	1.61	0.108
		q1	0.19	0.07	**2.95**	0.003	-0.15	0.07	**-2.25**	0.024	0.23	0.04	**5.95**	0.000	0.06	0.02	**3.54**	0.000	0.04	0.02	1.90	0.058

		q2	-0.02	0.04	-0.62	0.536	0.02	0.04	0.52	0.606	0.18	0.04	**4.01**	0.000	0.07	0.02	**3.03**	0.002	0.01	0.02	0.42	0.675
Fir Fruit Body	2012	q0																				
		q1																				
		q2																				
	2013	q0	-0.17	0.08	**-2.14**	0.033	0.05	0.06	0.82	0.415	0.02	0.07	0.25	0.806	-0.08	0.04	-1.77	0.076	0.15	0.05	**3.23**	0.001
		q1	-0.08	0.07	-1.11	0.267	0.10	0.08	1.18	0.239	0.11	0.05	**2.09**	0.036	-0.01	0.05	-0.21	0.836	0.08	0.05	1.45	0.147
		q2	0.03	0.04	0.84	0.399	-0.04	0.03	-1.28	0.199	0.10	0.07	1.47	0.141	-0.01	0.04	-0.30	0.766	0.07	0.05	1.40	0.161
	2015	q0	0.20	0.08	2.63	0.008	-0.01	0.10	-0.09	0.929	0.06	0.07	0.85	0.394	-0.01	0.04	-0.29	0.770	0.07	0.05	1.38	0.167
		q1	0.01	0.08	0.07	0.945	-0.22	0.08	**-2.83**	0.005	0.16	0.06	**2.77**	0.006	0.01	0.04	0.13	0.898	0.02	0.06	0.33	0.743
		q2	-0.02	0.03	-0.63	0.530	0.00	0.03	0.02	0.981	-0.16	0.11	-1.49	0.137	-0.07	0.05	-1.26	0.208	0.16	0.07	**2.24**	0.025
	2018	q0	0.30	0.11	**2.77**	0.006	-0.12	0.08	-1.53	0.126	-0.10	0.11	-0.87	0.383	-0.08	0.06	-1.35	0.178	0.15	0.07	1.96	0.050
		q1	0.17	0.10	1.77	0.077	-0.17	0.09	**-1.98**	0.047	0.07	0.09	0.82	0.412	-0.09	0.07	-1.24	0.215	0.12	0.08	1.55	0.122
		q2	0.00	0.03	0.01	0.989	-0.03	0.02	-1.13	0.258	0.22	0.08	**2.88**	0.004	0.02	0.05	0.46	0.646	-0.02	0.06	-0.26	0.797
	2021	q0	-0.09	0.09	-0.95	0.342	-0.03	0.09	-0.34	0.733	0.22	0.07	**2.96**	0.003	0.02	0.05	0.37	0.710	-0.01	0.06	-0.20	0.841
		q1	-0.08	0.09	-0.88	0.378	-0.02	0.08	-0.19	0.852	0.05	0.08	0.69	0.490	-0.06	0.05	-1.14	0.253	0.14	0.08	1.84	0.065
		q2	0.04	0.03	1.22	0.222	0.11	0.04	**2.51**	0.012	0.02	0.07	0.25	0.806	-0.08	0.04	-1.77	0.076	0.15	0.05	**3.23**	0.001

Influence of environmental factors on beta species diversity (community composition: Ord1, Ord2).

β - **SEM**				Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
				Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech metabarcoding	2012	Ord1	q0	0.24	0.07	**3.56**	0.000	0.01	0.03	0.27	0.788	-0.03	0.03	-0.82	0.410
			q1	0.33	0.12	**2.66**	0.008	0.13	0.06	**2.05**	0.040	-0.02	0.06	-0.31	0.753
			q2	-0.38	0.59	-0.65	0.515	0.23	0.29	0.78	0.435	-0.27	0.31	-0.90	0.371
		Ord2	q0	0.10	0.08	1.23	0.218	0.02	0.04	0.37	0.708	0.02	0.04	0.50	0.620
			q1	-0.10	0.16	-0.62	0.535	0.03	0.08	0.36	0.720	0.04	0.08	0.54	0.592
			q2	1.27	0.54	**2.36**	0.018	0.00	0.26	0.02	0.986	0.14	0.28	0.52	0.604
	2013	Ord1	q0	-0.40	0.03	**-15.45**	0.000	0.01	0.01	0.74	0.458	-0.02	0.01	-1.36	0.172
			q1	0.07	0.11	0.63	0.527	-0.01	0.05	-0.22	0.827	0.05	0.06	0.92	0.358
			q2	-0.11	0.34	-0.33	0.741	0.16	0.17	0.98	0.326	-0.01	0.18	-0.08	0.939
		Ord2	q0	0.00	0.06	-0.07	0.945	-0.03	0.03	-0.83	0.406	0.00	0.03	-0.01	0.990
			q1	-0.15	0.08	-1.85	0.064	0.02	0.04	0.61	0.543	0.01	0.04	0.13	0.897
			q2	0.33	0.32	1.05	0.292	-0.31	0.15	**-2.03**	0.043	0.17	0.17	1.00	0.318
	2015	Ord1	q0	-0.18	0.07	**-2.68**	0.007	-0.03	0.04	-0.93	0.351	0.02	0.03	0.71	0.480
			q1	0.25	0.13	1.91	0.056	0.07	0.07	0.94	0.349	-0.05	0.07	-0.70	0.487
			q2	0.04	0.39	0.09	0.928	0.08	0.21	0.38	0.703	0.12	0.20	0.60	0.552
		Ord2	q0	-0.11	0.06	-1.95	0.052	0.03	0.03	0.96	0.335	-0.04	0.03	-1.32	0.187
			q1	-0.04	0.10	-0.44	0.663	0.01	0.06	0.24	0.811	-0.07	0.05	-1.28	0.202
			q2	-0.32	0.38	-0.84	0.398	0.29	0.21	1.42	0.157	-0.39	0.20	**-1.98**	0.047

	2018	Ord1	q0	0.44	0.04	**12.37**	0.000	-0.01	0.02	-0.57	0.567	0.03	0.02	1.46	0.144
			q1	0.45	0.09	**5.15**	0.000	0.04	0.04	0.99	0.321	0.04	0.05	0.82	0.411
			q2	-0.15	0.33	-0.45	0.650	0.13	0.16	0.83	0.405	0.05	0.18	0.26	0.795
		Ord2	q0	0.00	0.06	-0.02	0.983	-0.04	0.03	-1.21	0.228	0.04	0.03	1.18	0.238
			q1	0.22	0.10	**2.33**	0.020	-0.04	0.05	-0.96	0.338	0.04	0.05	0.80	0.423
			q2	0.39	0.30	1.29	0.196	-0.11	0.14	-0.77	0.441	0.35	0.16	**2.21**	0.027
	2021	Ord1	q0	0.40	0.02	**16.49**	0.000	0.02	0.01	1.69	0.092	-0.01	0.01	-0.77	0.443
			q1	-0.35	0.10	**-3.49**	0.000	0.03	0.05	0.58	0.564	-0.01	0.05	-0.28	0.783
			q2	-0.16	0.36	-0.45	0.653	0.06	0.17	0.37	0.708	-0.22	0.19	-1.17	0.241
		Ord2	q0	-0.07	0.06	-1.27	0.203	0.02	0.03	0.67	0.500	-0.02	0.03	-0.74	0.459
			q1	0.31	0.08	**3.94**	0.000	0.02	0.04	0.64	0.524	0.01	0.04	0.35	0.724
			q2	0.26	0.31	0.85	0.397	-0.40	0.15	**-2.69**	0.007	0.13	0.16	0.81	0.415
Fir metabarcoding	2012	Ord1	q0	0.13	0.06	**2.09**	0.037	0.07	0.04	1.60	0.110	-0.14	0.05	**-2.73**	0.006
			q1	-0.14	0.10	-1.43	0.152	0.15	0.07	**2.21**	0.027	-0.19	0.09	**-2.28**	0.023
			q2	0.08	0.33	0.24	0.807	-0.02	0.23	-0.09	0.928	-0.34	0.29	-1.17	0.241
		Ord2	q0	0.22	0.05	**4.18**	0.000	0.00	0.04	0.08	0.939	0.05	0.04	1.12	0.263
			q1	0.09	0.12	0.76	0.445	0.15	0.09	1.75	0.081	-0.20	0.11	-1.85	0.065
			q2	-0.06	0.34	-0.17	0.866	0.33	0.24	1.40	0.161	-0.15	0.29	-0.53	0.594
	2013	Ord1	q0	0.32	0.03	**9.92**	0.000	-0.01	0.02	-0.38	0.701	-0.02	0.03	-0.69	0.489
			q1	0.37	0.08	**4.67**	0.000	-0.05	0.06	-0.92	0.358	0.03	0.07	0.37	0.708
			q2	0.16	0.38	0.43	0.664	-0.07	0.27	-0.24	0.807	0.52	0.32	1.61	0.107
		Ord2	q0	0.03	0.07	0.37	0.711	-0.01	0.05	-0.13	0.895	0.02	0.06	0.27	0.788

			q1	0.10	0.08	1.37	0.172	0.00	0.05	0.04	0.965	-0.04	0.07	-0.64	0.524
			q2	0.09	0.39	0.23	0.821	0.15	0.27	0.55	0.579	0.09	0.33	0.26	0.792
	2015	Ord1	q0	0.02	0.08	0.20	0.840	-0.04	0.06	-0.69	0.492	0.07	0.07	1.04	0.298
			q1	0.08	0.15	0.54	0.586	-0.02	0.11	-0.19	0.849	0.06	0.13	0.45	0.653
			q2	0.52	0.43	1.20	0.232	-0.08	0.31	-0.25	0.804	-0.06	0.38	-0.15	0.879
		Ord2	q0	0.07	0.06	1.06	0.288	-0.06	0.04	-1.30	0.195	0.09	0.05	1.63	0.102
			q1	0.02	0.10	0.23	0.815	-0.14	0.07	-1.94	0.052	0.27	0.08	**3.30**	0.001
			q2	0.03	0.47	0.06	0.952	0.12	0.34	0.34	0.736	-0.36	0.41	-0.88	0.377
	2018	Ord1	q0	0.37	0.06	**6.42**	0.000	0.02	0.04	0.41	0.682	-0.03	0.05	-0.55	0.585
			q1	0.36	0.09	**3.93**	0.000	-0.07	0.06	-1.12	0.261	0.09	0.08	1.11	0.269
			q2	-0.05	0.36	-0.14	0.885	-0.25	0.25	-0.99	0.320	0.07	0.31	0.21	0.830
		Ord2	q0	-0.04	0.06	-0.69	0.490	0.11	0.04	**2.40**	0.016	-0.07	0.05	-1.29	0.196
			q1	0.20	0.10	1.96	0.050	0.11	0.07	1.61	0.108	-0.10	0.09	-1.17	0.241
			q2	-0.42	0.31	-1.33	0.185	-0.08	0.22	-0.37	0.715	0.53	0.27	**2.00**	0.046
	2021	Ord1	q0	0.36	0.04	**9.42**	0.000	0.01	0.03	0.25	0.799	0.03	0.03	0.93	0.351
			q1	-0.24	0.11	**-2.13**	0.033	0.20	0.08	**2.56**	0.010	-0.15	0.10	-1.51	0.132
			q2	-0.09	0.35	-0.25	0.803	0.17	0.25	0.70	0.482	0.03	0.30	0.08	0.934
		Ord2	q0	0.03	0.07	0.39	0.694	0.02	0.05	0.40	0.690	-0.06	0.06	-1.03	0.303
			q1	-0.26	0.11	**-2.44**	0.015	-0.09	0.08	-1.16	0.245	0.09	0.09	0.92	0.359
			q2	-0.11	0.30	-0.35	0.727	-0.54	0.22	**-2.51**	0.012	0.70	0.26	**2.66**	0.008
	2012	Ord1	q0	-0.53	0.10	**-5.23**	0.000	-0.05	0.05	-0.94	0.345	0.00	0.04	-0.03	0.978
			q1	-0.47	0.12	**-4.08**	0.000	-0.03	0.06	-0.51	0.611	-0.04	0.05	-0.72	0.471

Beech fruit body			q2	0.03	0.52	0.05	0.957	-0.12	0.25	-0.49	0.623	0.12	0.23	0.51	0.610
		Ord2	q0	0.10	0.14	0.70	0.485	-0.02	0.07	-0.25	0.804	0.03	0.06	0.48	0.631
			q1	-0.06	0.11	-0.59	0.554	0.04	0.05	0.79	0.430	-0.15	0.05	**-3.31**	0.001
			q2	-0.08	0.46	-0.18	0.858	-0.24	0.22	-1.08	0.282	-0.03	0.20	-0.16	0.876
	2013	Ord1	q0	0.61	0.11	**5.47**	0.000	0.06	0.05	1.18	0.239	-0.01	0.06	-0.15	0.880
			q1	0.52	0.10	**5.43**	0.000	0.07	0.05	1.52	0.128	0.01	0.05	0.20	0.838
			q2	-0.22	0.31	-0.72	0.473	0.15	0.15	1.01	0.311	-0.24	0.16	-1.49	0.137
		Ord2	q0	0.18	0.13	1.32	0.186	-0.02	0.06	-0.29	0.774	0.02	0.07	0.25	0.800
			q1	0.11	0.11	0.97	0.330	0.02	0.06	0.29	0.773	0.00	0.06	0.04	0.972
			q2	-0.12	0.32	-0.37	0.711	0.14	0.16	0.91	0.365	-0.04	0.17	-0.27	0.789
	2015	Ord1	q0	0.57	0.09	**6.64**	0.000	0.01	0.04	0.23	0.817	0.07	0.05	1.54	0.123
			q1	0.51	0.08	**6.54**	0.000	-0.02	0.04	-0.42	0.677	0.06	0.04	1.43	0.154
			q2	-0.09	0.27	-0.34	0.734	0.10	0.13	0.78	0.435	-0.06	0.14	-0.41	0.681
		Ord2	q0	0.08	0.10	0.78	0.435	0.04	0.05	0.85	0.396	-0.05	0.05	-1.02	0.308
			q1	0.07	0.07	1.00	0.316	0.03	0.03	0.81	0.418	-0.11	0.04	-3.12	0.002
			q2	0.06	0.26	0.25	0.803	-0.03	0.13	-0.23	0.819	0.20	0.14	1.43	0.154
	2018	Ord1	q0	0.55	0.07	**7.63**	0.000	-0.04	0.04	-1.22	0.224	0.07	0.04	1.75	0.080
			q1	0.49	0.06	**8.61**	0.000	-0.04	0.03	-1.50	0.135	0.07	0.03	**2.25**	0.024
			q2	-0.10	0.21	-0.47	0.638	-0.06	0.11	-0.54	0.586	-0.06	0.11	-0.54	0.592
		Ord2	q0	0.02	0.09	0.18	0.859	0.05	0.05	1.03	0.303	-0.05	0.05	-0.97	0.330
			q1	0.01	0.10	0.08	0.933	0.01	0.05	0.28	0.783	0.02	0.05	0.40	0.691
			q2	-0.01	0.21	-0.07	0.945	-0.03	0.11	-0.33	0.742	-0.10	0.11	-0.87	0.384

	2021	Ord1	q0	-0.03	0.12	-0.22	0.828	0.05	0.06	0.82	0.410	-0.18	0.06	**-2.82**	0.005
			q1	-0.17	0.12	-1.46	0.144	0.05	0.06	0.77	0.440	-0.16	0.06	**-2.57**	0.010
			q2	0.17	0.26	0.67	0.505	-0.09	0.13	-0.72	0.473	0.00	0.14	-0.01	0.989
		Ord2	q0	-0.03	0.12	-0.22	0.828	-0.03	0.06	-0.45	0.653	-0.04	0.06	-0.58	0.561
			q1	0.15	0.11	1.30	0.195	0.01	0.06	0.12	0.901	0.02	0.06	0.34	0.735
			q2	-0.04	0.25	-0.15	0.885	0.07	0.13	0.58	0.564	-0.18	0.13	-1.31	0.191
Fir fruit body	2012	Ord1	q0												
			q1												
			q2												
		Ord2	q0												
			q1												
			q2												
	2013	Ord1	q0	-0.74	0.15	**-4.84**	0.000	-0.18	0.12	-1.50	0.134	0.19	0.14	1.42	0.157
			q1	-0.57	0.19	**-3.01**	0.003	-0.19	0.15	-1.23	0.217	0.16	0.17	0.91	0.361
			q2	0.19	0.34	0.54	0.588	-0.71	0.28	**-2.58**	0.010	0.73	0.31	**2.35**	0.019
		Ord2	q0	0.02	0.20	0.10	0.920	0.03	0.16	0.17	0.863	-0.05	0.18	-0.28	0.778
			q1	0.33	0.16	**2.04**	0.041	0.10	0.13	0.80	0.426	-0.13	0.14	-0.92	0.358
			q2	0.53	0.41	1.30	0.195	0.45	0.33	1.36	0.173	-0.59	0.37	-1.61	0.108
	2015	Ord1	q0	0.31	0.15	**2.11**	0.035	0.07	0.11	0.64	0.523	-0.19	0.14	-1.40	0.160
			q1	0.51	0.14	**3.73**	0.000	-0.10	0.10	-0.96	0.338	0.08	0.13	0.61	0.543
			q2	0.17	0.42	0.42	0.676	0.11	0.31	0.36	0.722	-0.57	0.38	-1.50	0.134
		Ord2	q0	0.38	0.12	**3.33**	0.001	-0.12	0.09	-1.41	0.158	0.07	0.11	0.63	0.528

			q1	-0.43	0.14	**-2.96**	0.003	-0.07	0.11	-0.64	0.521	0.17	0.13	1.28	0.202
			q2	0.09	0.45	0.20	0.839	-0.18	0.33	-0.54	0.588	0.08	0.41	0.20	0.844
	2018	Ord1	q0	0.77	0.15	**4.99**	0.000	0.05	0.12	0.44	0.657	-0.20	0.15	-1.39	0.166
			q1	0.85	0.18	**4.64**	0.000	0.09	0.14	0.65	0.514	-0.24	0.18	-1.34	0.179
			q2	0.93	0.65	1.44	0.150	0.84	0.50	1.70	0.089	-0.34	0.62	-0.55	0.580
		Ord2	q0	0.01	0.21	0.05	0.961	0.17	0.16	1.05	0.293	-0.16	0.21	-0.78	0.435
			q1	-0.11	0.21	-0.55	0.582	0.07	0.16	0.43	0.664	-0.06	0.20	-0.30	0.761
			q2	0.10	0.82	0.12	0.904	-0.41	0.62	-0.66	0.507	0.26	0.78	0.33	0.739
	2021	Ord1	q0	0.40	0.16	**2.42**	0.015	-0.10	0.12	-0.84	0.400	-0.08	0.16	-0.48	0.628
			q1	0.38	0.16	**2.42**	0.016	-0.13	0.12	-1.09	0.274	-0.06	0.15	-0.39	0.698
			q2	0.49	0.42	1.16	0.245	0.28	0.31	0.90	0.366	-0.67	0.41	-1.65	0.100
		Ord2	q0	-0.20	0.17	-1.20	0.229	0.15	0.12	1.22	0.221	-0.11	0.16	-0.69	0.493
			q1	-0.08	0.18	-0.42	0.674	0.17	0.13	1.28	0.201	-0.10	0.17	-0.56	0.577
			q2	1.11	0.32	**3.46**	0.001	0.73	0.24	**3.06**	0.002	-1.15	0.31	**-3.69**	0.000

Tab S. 9 Structural equation models, based on species data aggregated across years, illustrating the influence of environmental factors and alpha species diversity (qD, estimated species richness) on deadwood density loss. Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, t= t-value, p= p-value, mb= metabarcoding, fb= fruit body.

α – **SEM**		Species diversity				Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
		Est	se	t	p	Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech mb	q0	0.04	0.14	0.30	0.765	0.17	0.05	**3.59**	0.000	0.08	0.02	**3.19**	0.001	0.01	0.02	0.28	0.779
	q1	0.19	0.82	0.23	0.818	0.17	0.05	**3.65**	0.000	0.08	0.02	**3.14**	0.002	0.01	0.02	0.28	0.778
	q2	0.03	0.14	0.20	0.839	0.17	0.05	**3.69**	0.000	0.08	0.02	**3.13**	0.002	0.01	0.02	0.28	0.776
Fir mb	q0	-0.22	0.14	-1.57	0.117	0.16	0.05	**3.04**	0.002	0.00	0.04	-0.14	0.888	0.08	0.05	1.45	0.148
	q1	-1.27	0.87	-1.47	0.141	0.16	0.05	**3.00**	0.003	0.00	0.04	-0.13	0.898	0.07	0.05	1.39	0.164
	q2	-0.19	0.15	-1.26	0.207	0.16	0.05	**2.89**	0.004	0.00	0.04	-0.13	0.898	0.07	0.05	1.29	0.196
Beech fb	q0	-0.11	0.09	-1.21	0.228	0.18	0.04	**4.13**	0.000	0.08	0.02	**3.32**	0.001	0.01	0.02	0.45	0.654
	q1	-0.10	0.09	-1.06	0.287	0.18	0.04	**4.12**	0.000	0.08	0.02	**3.36**	0.001	0.01	0.02	0.46	0.642
	q2	-0.09	0.10	-0.89	0.371	0.19	0.05	**4.05**	0.000	0.08	0.02	**3.36**	0.001	0.01	0.02	0.46	0.644
Fir fb	q0	-0.16	0.07	**-2.32**	0.020	0.16	0.05	**3.22**	0.001	-0.02	0.03	-0.65	0.515	0.05	0.05	1.03	0.304
	q1	-0.18	0.08	**-2.38**	0.017	0.15	0.05	**3.07**	0.002	-0.02	0.03	-0.65	0.517	0.04	0.05	0.98	0.330
	q2	-0.18	0.08	**-2.22**	0.027	0.14	0.05	**2.78**	0.005	-0.02	0.03	-0.58	0.559	0.04	0.05	0.92	0.356

Influence of environmental factors on alpha species diversity (qD, estimated species richness).

α – **SEM**		Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
		Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech mb	q0	0.11	0.07	1.55	0.120	-0.04	0.04	-1.16	0.247	0.00	0.04	0.11	0.913
	q1	0.02	0.01	1.44	0.150	-0.01	0.01	-1.36	0.175	0.00	0.01	0.11	0.915
	q2	0.09	0.07	1.28	0.201	-0.05	0.04	-1.37	0.170	0.00	0.04	0.06	0.954
Fir mb	q0	0.10	0.08	1.28	0.201	0.01	0.05	0.21	0.833	0.12	0.08	1.56	0.118
	q1	0.02	0.01	1.23	0.220	0.00	0.01	0.26	0.798	0.02	0.01	1.46	0.143
	q2	0.08	0.08	1.08	0.281	0.02	0.05	0.29	0.771	0.10	0.07	1.34	0.179
Beech fb	q0	0.05	0.11	0.49	0.621	0.00	0.06	0.02	0.986	0.03	0.06	0.59	0.554
	q1	0.10	0.10	0.95	0.340	0.02	0.05	0.33	0.743	0.04	0.05	0.76	0.449
	q2	0.14	0.10	1.47	0.142	0.03	0.05	0.63	0.531	0.05	0.05	0.92	0.358
Fir fb	q0	0.11	0.16	0.74	0.459	-0.09	0.11	-0.86	0.388	-0.01	0.15	-0.05	0.958
	q1	0.05	0.14	0.33	0.744	-0.08	0.10	-0.83	0.407	-0.02	0.13	-0.16	0.869
	q2	-0.02	0.13	-0.16	0.870	-0.07	0.09	-0.76	0.445	-0.03	0.12	-0.25	0.802

Tab S. 10 Structural equation models, based on species data aggregated across years, illustrating the influence of environmental factors and beta species diversity (community composition) on deadwood density loss. Community composition was represented by vector predictors using the species scores from the first two axes (Ord1, Ord2) of the Principal Coordinates Analyses (see Method section). Models were conducted for each combination of tree species, sampling method, and diversity measures. Bold values indicate significant effects (p-value < 0.05). Est= estimate, se= standard error, t= t-value, p= p-value, mb= metabarcoding, fb= fruit body.

β – **SEM**		Species diversity								Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
		Ord1				Ord2															
		Est	se	t	p	Est	se	t	p	Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech mb	q0	-0.26	0.27	-0.95	0.341	-0.34	0.15	-2.22	0.027	0.29	0.10	2.86	0.004	0.07	0.02	2.90	0.004	0.02	0.02	0.72	0.472
	q1	-0.12	0.33	-0.37	0.714	-0.21	0.17	-1.22	0.222	0.22	0.12	1.79	0.074	0.07	0.02	2.98	0.003	0.01	0.02	0.49	0.623
	q2	0.23	0.05	4.51	0.000	0.04	0.05	0.76	0.448	0.15	0.03	4.57	0.000	0.09	0.02	5.54	0.000	-0.04	0.02	-2.10	0.035
Fir mb	q0	0.79	0.32	**2.44**	0.014	0.28	0.14	**1.99**	0.046	-0.09	0.10	-0.91	0.361	0.00	0.03	-0.03	0.974	0.06	0.04	1.40	0.162
	q1	0.66	0.38	1.74	0.082	0.26	0.16	1.63	0.104	-0.07	0.13	-0.54	0.593	0.00	0.03	-0.03	0.976	0.05	0.05	1.15	0.252
	q2	-0.21	0.10	**-2.00**	0.045	-0.15	0.10	-1.60	0.110	0.14	0.05	**2.91**	0.004	-0.02	0.03	-0.70	0.485	0.04	0.05	0.76	0.445
Beech fb	q0	0.352	0.27	1.33	0.185	0.04	0.13	0.34	0.732	0.01	0.13	0.07	0.944	0.06	0.03	**2.56**	0.010	-0.01	0.03	-0.25	0.805
	q1	-0.14	0.25	-0.57	0.571	-0.27	0.15	-1.88	0.060	0.238	0.11	**2.06**	0.039	0.08	0.02	**3.69**	0.000	0.01	0.02	0.35	0.728
	q2	-0.03	0.05	-0.68	0.496	0.05	0.05	1.20	0.232	0.18	0.04	**4.10**	0.000	0.07	0.02	**3.03**	0.002	0.01	0.02	0.41	0.679
Fir fb	q0	-0.33	0.15	**-2.21**	0.027	-0.02	0.12	-0.16	0.876	-0.03	0.09	-0.24	0.813	-0.01	0.03	-0.12	0.906	0.07	0.05	1.52	0.129
	q1	0.11	0.12	0.88	0.377	0.22	0.11	**2.01**	0.044	0.08	0.08	0.93	0.355	0.00	0.04	-0.00	0.998	0.05	0.05	1.01	0.315
	q2	0.05	0.02	**2.14**	0.032	0.02	0.02	0.67	0.505	0.17	0.05	**3.34**	0.001	0.00	0.04	0.01	0.996	0.04	0.05	0.80	0.453

Influence of environmental factors on beta species diversity (community composition: Ord1, Ord2).

β - SEM			Canopy cover = open				Deadwood heterogeneity				Deadwood amount			
			Est	se	t	p	Est	se	t	p	Est	se	t	p
Beech mb	Ord1	q0	0.34	0.03	**10.12**	0.000	0.01	0.02	0.33	0.744	-0.01	0.02	-0.44	0.662
		q1	0.36	0.03	**12.29**	0.000	0.00	0.02	0.20	0.844	0.03	0.03	1.08	0.279
		q2	0.12	0.13	0.92	0.358	-0.08	0.07	-1.18	0.237	0.00	0.02	-0.32	0.746
	Ord2	q0	0.09	0.06	1.43	0.154	-0.03	0.03	-1.10	0.269	0.03	0.03	0.86	0.387
		q1	0.03	0.06	0.45	0.652	-0.03	0.03	-1.04	0.299	0.21	0.07	**3.02**	0.003
		q2	-0.01	0.14	-0.08	0.939	0.01	0.07	0.09	0.925	-0.02	0.07	-0.24	0.812
Fir mb	Ord1	q0	0.29	0.03	**9.15**	0.000	-0.01	0.02	-0.66	0.510	0.00	0.03	-0.15	0.883
		q1	0.30	0.03	**10.83**	0.000	-0.01	0.02	-0.70	0.483	-0.03	0.07	-0.50	0.616
		q2	0.02	0.10	0.16	0.869	-0.05	0.07	-0.66	0.511	0.00	0.03	-0.07	0.942
	Ord2	q0	0.03	0.07	0.45	0.651	0.02	0.05	0.34	0.735	-0.01	0.06	-0.21	0.831
		q1	0.02	0.07	0.33	0.743	0.01	0.05	0.21	0.836	-0.10	0.09	-1.02	0.309
		q2	-0.03	0.11	-0.27	0.784	-0.04	0.08	-0.56	0.578	0.05	0.10	0.45	0.652
Beech fb	Ord1	q0	0.47	0.04	**13.27**	0.000	0.02	0.02	1.30	0.192	0.04	0.02	**2.22**	0.026
		q1	0.42	0.04	**11.57**	0.000	0.02	0.02	0.79	0.429	0.04	0.02	1.92	0.054
		q2	0.05	0.20	0.27	0.785	-0.10	0.11	-0.90	0.366	0.18	0.10	1.70	0.089
	Ord2	q0	-0.01	0.07	-0.18	0.858	0.07	0.04	1.68	0.093	-0.03	0.04	-0.89	0.375
		q1	-0.01	0.06	-0.18	0.861	0.01	0.03	0.40	0.689	-0.01	0.03	-0.42	0.675
		q2	0.00	0.21	0.01	0.996	0.05	0.110	0.417	0.677	0.05	0.11	0.42	0.674

Fir fb	Ord1	q0	-0.49	0.07	**-6.96**	0.000	0.01	0.05	0.22	0.828	0.07	0.07	1.09	0.274
		q1	0.52	0.09	**5.91**	0.000	-0.08	0.06	-1.39	0.164	0.02	0.08	0.23	0.816
		q2	-0.64	0.47	-1.35	0.178	-0.05	0.33	-0.14	0.890	0.03	0.45	0.07	0.946
	Ord2	q0	0.13	0.09	1.45	0.147	0.00	0.06	0.01	0.988	-0.03	0.09	-0.34	0.731
		q1	0.03	0.10	0.35	0.728	0.01	0.07	0.12	0.906	-0.01	0.09	-0.06	0.949
		q2	0.04	0.46	0.09	0.929	-0.36	0.32	-1.13	0.257	0.68	0.44	1.54	0.123

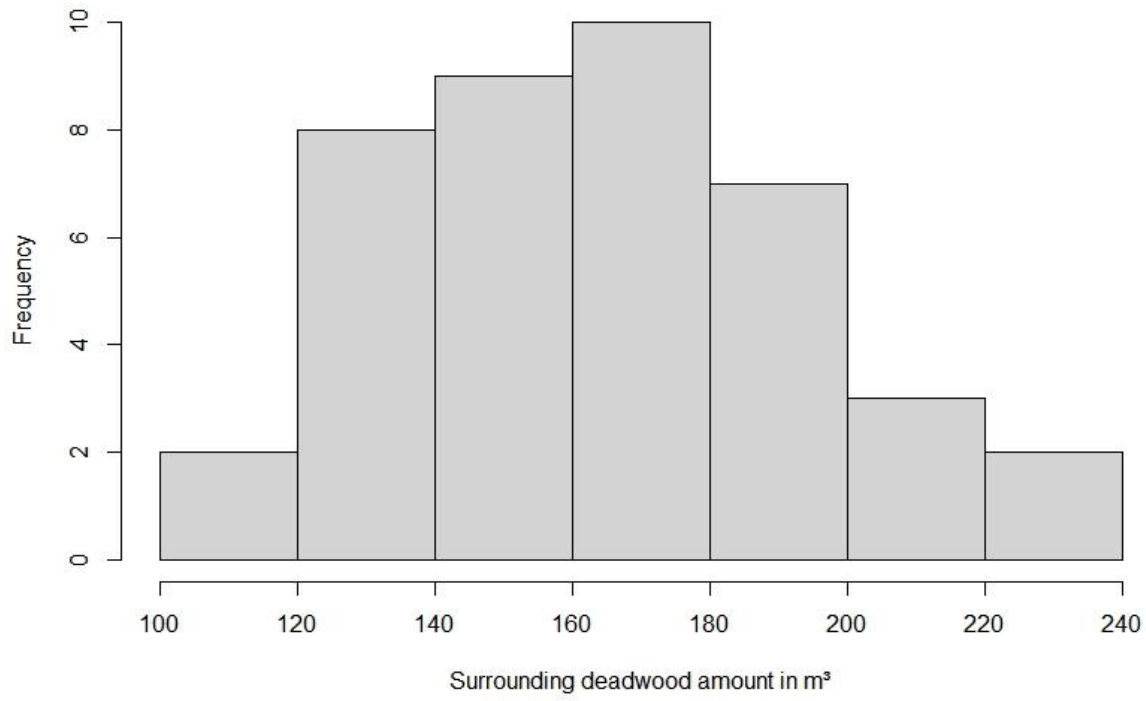

Fig. S1 Distribution of the surrounding deadwood amount.

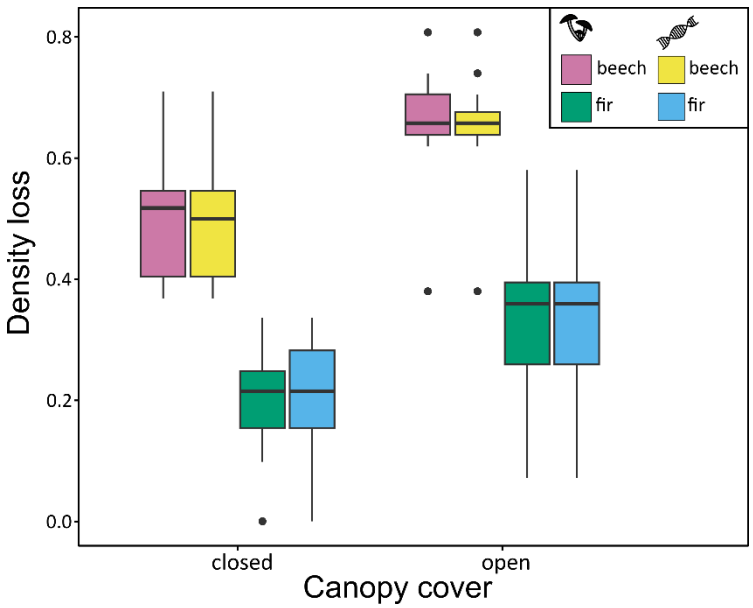

Fig. S2 Deadwood density loss in beech and fir under closed and open canopies, with fungal diversity detected via fruit body surveys (fungal pictogram) and metabarcoding (DNA double helix pictogram). Visualization based on the analysis separated by sampling method and tree species. Differences in the number of logs are due to the presence or absence of species (e.g., fruit body data on fir logs in 2012).

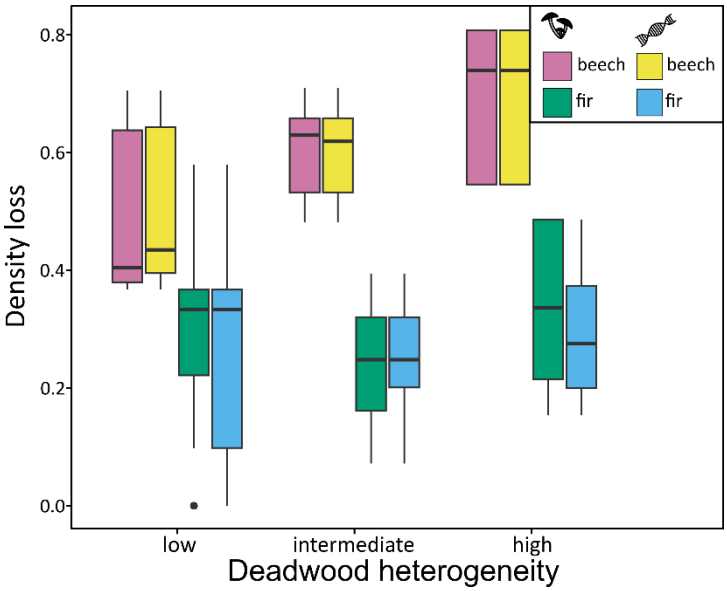

Fig. S3 Density loss in plots with varying deadwood heterogeneity, where fungal diversity was detected using two sampling methods: fruit body surveys (fungal pictogram) and metabarcoding (DNA double helix pictogram). Visualization based on the analysis separated by sampling method and tree species. Differences in the number of logs are due to the presence or absence of species (e.g., fruit body data on fir logs in 2012). The lowest heterogeneity level includes only one of the four substrate types (fir branches, fir logs, beech branches, or beech logs). The intermediate level includes either one tree species with both diameter classes (e.g., fir logs and fir branches or beech logs and beech branches) or both tree species with one diameter class (e.g., fir and beech logs or fir and beech branches). The highest heterogeneity level combines both tree species and both diameter classes. Deadwood heterogeneity was indexed based on substrate diversity per plot, following Siitonen et al. (2000).

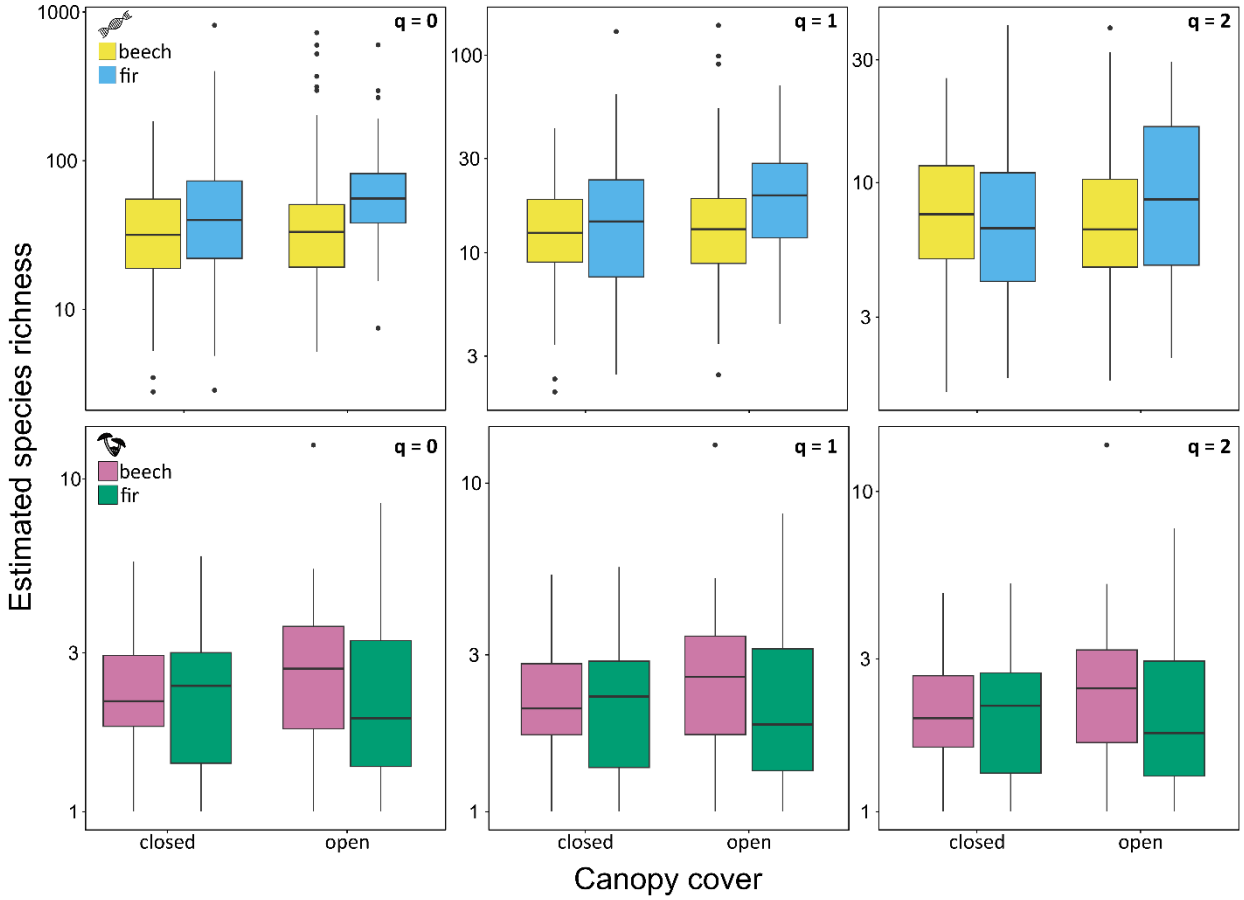

Fig. S4 Estimated species richness (alpha diversity) for rare (q=0), common (q=1), and dominant (q=2) species on beech and fir logs in closed and open canopies. Fungal species were detected using two sampling methods: metabarcoding (DNA double helix pictogram, first row) and fruit body surveys (fungal pictogram, second row).

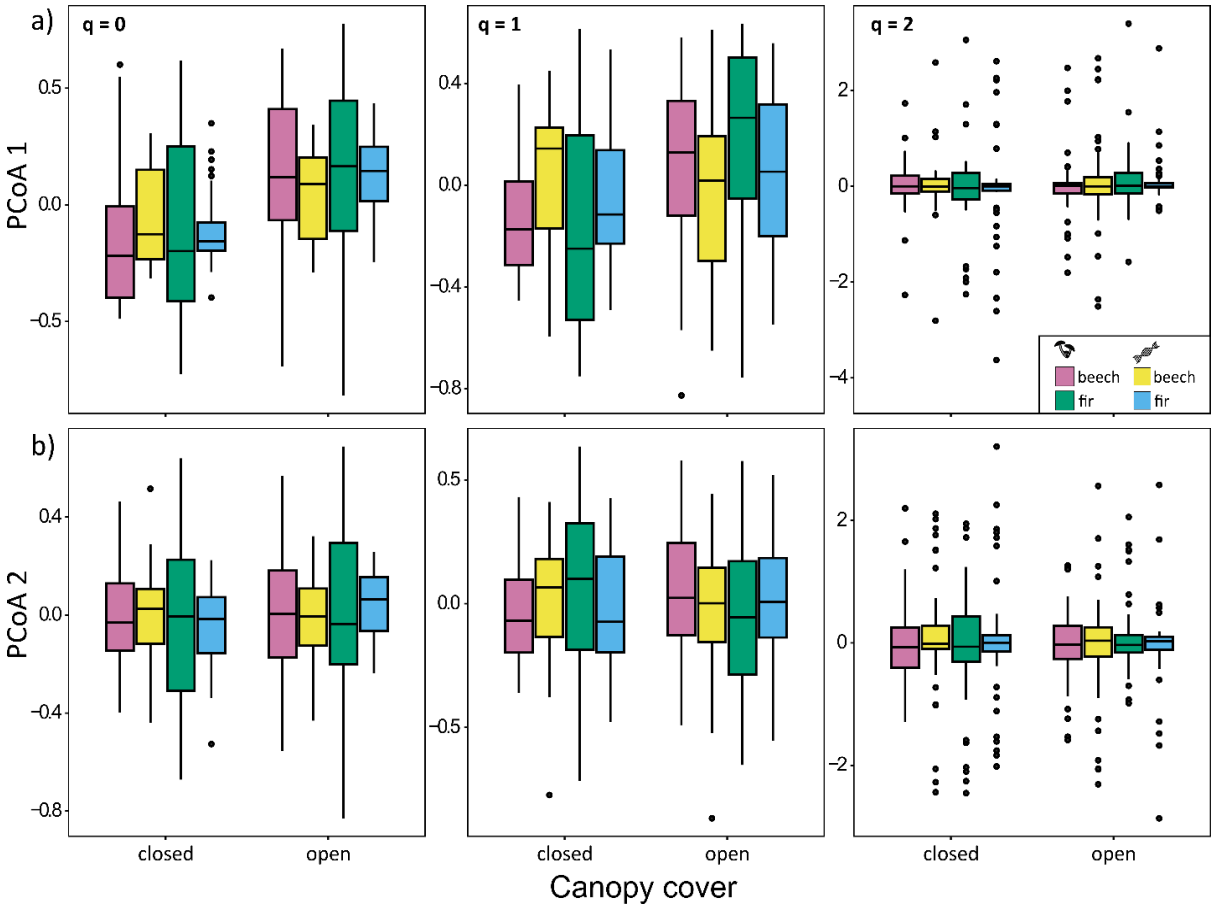

Fig. S5 Community composition (beta diversity, represented by the first two axes of a Principal Coordinates Analyses (first axis PCoA1; second axis: PCoA2) for rare (q=0), common (q=1), and dominant (q=2) species on beech and fir logs in closed and open canopies. Fungal species were detected using two sampling methods: fruit body surveys (fungal pictogram) and metabarcoding (DNA double helix pictogram).

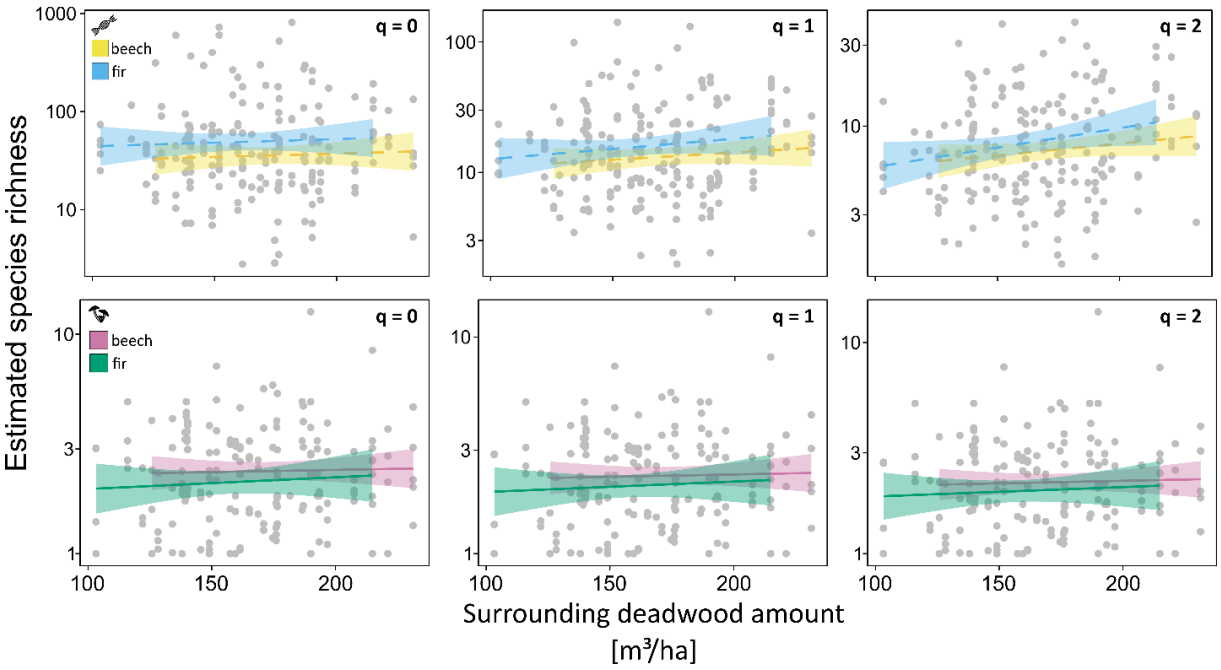

Fig. S6 Estimated species richness (alpha diversity) for rare (q=0), common (q=1), and dominant (q=2) species on beech and fir logs across plots with varying amounts of surrounding deadwood. Fungal species were detected using two sampling methods: metabarcoding (DNA double helix pictogram, first row) and fruit body surveys (fungal pictogram, second row). Solid lines denote significant, and dashed lines non-significant, effect sizes from meta-analyses of the structural equation models (see caption of figure 3 in the main text).

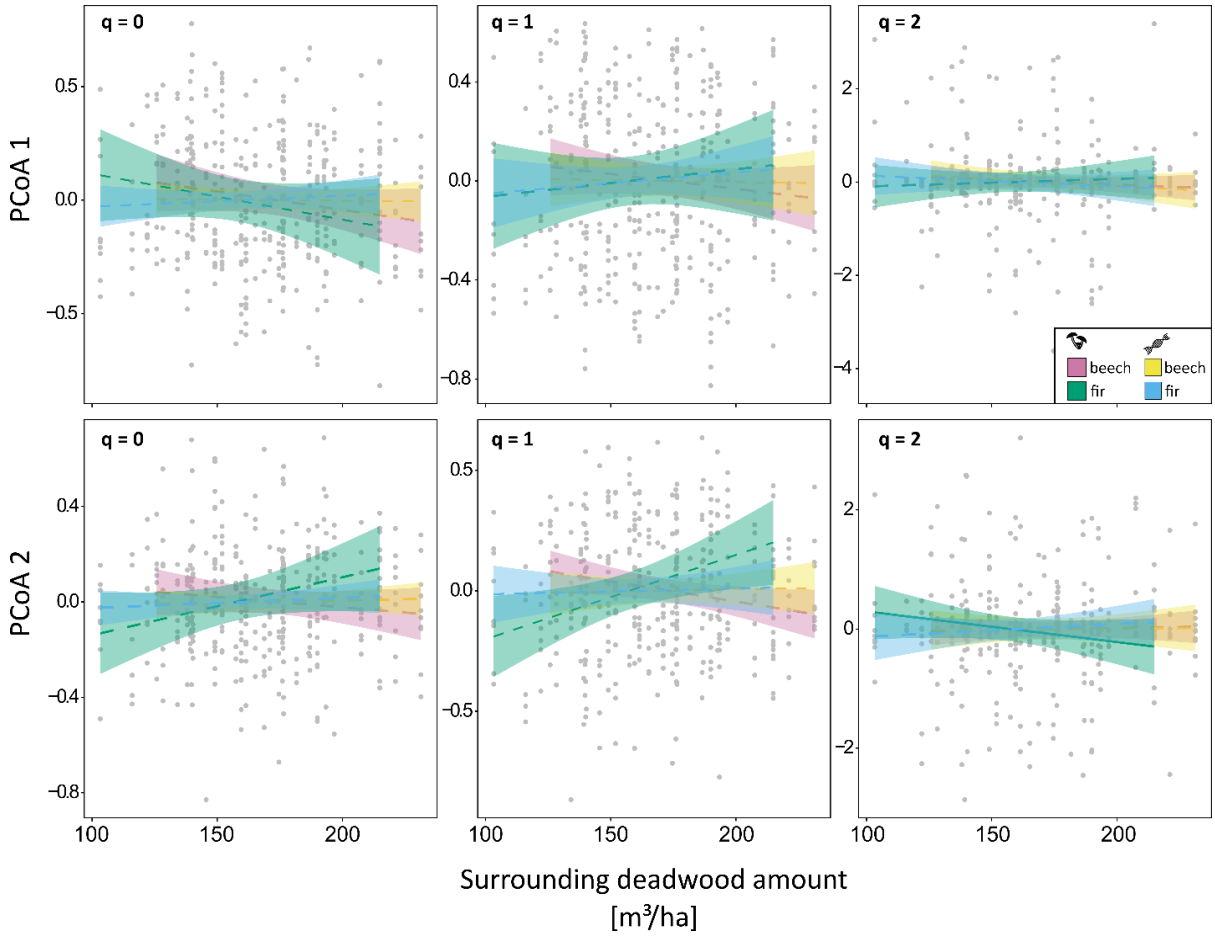

Fig. S7 Community composition (beta diversity, represented by the first two axes of a Principal Coordinates Analyses (first axis PCoA1; second axis: PCoA2) for rare (q=0), common (q=1), and dominant (q=2) species on beech and fir logs across plots with varying amounts of surrounding deadwood. Fungal species were detected using two sampling methods: fruit body surveys (fungal pictogram) and metabarcoding (DNA double helix pictogram). Solid lines denote significant, and dashed lines non-significant, effect sizes from meta-analyses of the structural equation models (see caption of figure 3 in the main text).

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12 DECLARATIONS

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