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Effects of forest management on the key fungal decomposer *Fomes fomentarius* in European beech forests – Lessons from a large-scale experiment

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ABSTRACT

Fomes fomentarius (L.) Fr., (commonly known as Tinder fungus) is an abundant fungus in European beech old-growth forests and is important for nutrient cycles, food web dynamics, and biodiversity. The species was heavily reduced during the last centuries by forestry. Modern silviculture strategies in Central Europe aim to balance both the extraction of wood and promoting dead wood habitats. Such an approach is key to sustaining *Fomes fomentarius* as well as up to 600 saproxylic arthropods associated with the fungus. The aim of this study was to assess how dead wood type in combination with microclimate, resulting from different forest management strategies, affect the presence (occupancy) and abundance (percent cover occupied) of *Fomes fomentarius* fruit bodies at the stand- and dead wood object-scale. We experimentally extracted a standardized proportion of trees within 50 m by 50 m patches creating stumps, logs, snags, and logs with snags under two microclimate treatments (open canopy gap versus closed canopy) in a random block design. As a control, we defined cut stumps under closed canopies, as this is the common thinning approach in mature beech production forests. We tested the effects of alternative management strategies against the control using Generalized Linear Mixed-effects Models. At the stand-scale, our model revealed a significantly lower occupancy of *Fomes fomentarius* in control stands compared to treatments in which dead wood was not removed. The average cover of *Fomes fomentarius* on snags under a closed canopy, at both the stand- and dead wood object-scale, was higher than in control plots. However, effect size was weak at the object-scale. To increase this principal decomposer and boost important microhabitats for many arthropods, silviculture should aim to increase snags while maintaining dense forest canopies. Yet, at landscape scale, diversifying dead wood types and light conditions may boost overall saproxylic diversity.

1. Introduction

The aim of multifunctional forestry can be viewed as the sustainable use of forest products like timber while maintaining biodiversity and other important ecosystem processes (Gren and Amuakwa-Mensah, 2019). Among the most important structures that determine biodiversity in forests is dead wood (Esseen et al., 1997; Stokland et al., 2012; Yang et al., 2021; Moreira-Arce et al., 2021; Graf et al., 2022) and standing senescent habitat trees (DeMars et al., 2010; Lindenmayer et al., 2012). However, there is a clear trade-off between the extraction of timber and retaining dead wood in the forest to support dead wood-dependent diversity and subsequent decomposition processes that

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maintain the carbon and nutrient cycles. Since the 2000 s, most forestry concepts in Central Europe have considered dead wood to be an important diversity feature (Yang et al., 2021). Yet species depending on dead wood are still suppressed by common management activities (Stokland et al., 2012; Thorn et al., 2020). Therefore, we need to further develop efficient forest management concepts to optimize both the use of timber and the maintenance of wood-dependent key species, diversity, and related ecosystem processes (Sandström et al., 2019).

Wood-decaying fungi are among the most diverse taxa of dead wood (Stokland et al., 2012). With their uniquely evolved enzymatic portfolio, fungi are the main (Tlalka et al., 2008; Větrovský et al., 2011) and most efficient wood decomposers (e.g., of lignin, in Floudas et al., 2012). Fungi, as essential decomposers, are thus crucial to the global carbon and nutrient cycles (Baldrian, 2017; Johnston et al., 2016; Jomura et al., 2022; Cornwell et al., 2009). Particularly abundant decomposer species play a pivotal role in the breakdown of dead wood (Fagerli Lunde et al., 2023). In European beech (*Fagus sylvatica*) forests, the dominant natural forest type in Central Europe (Baum et al., 2003), *Fomes fomentarius* is an abundant polypore, and thus among the most important wood-decaying fungi. *Fomes fomentarius* is a white-rot basidiomycete ("enzymatically the most totally equipped of all decomposers," Swift et al., 1979) and hence able to break down the recalcitrant lignin (Stokland et al., 2012; Schmidt, 2006). *Fomes fomentarius* has a wide distribution in temperate and boreal forests, particularly in the northern hemisphere (GBIF Secretariat, 2022). Although it is abundant and has a wide distribution, logging practices can limit the mycelial development and fruiting body formation of *Fomes fomentarius* and, in some cases, has caused its regional extinction (Zytynska et al., 2018). However, the case study of Zytynska et al. (2018), has shown that after being extinct for half a century, the fungus was able to return to the researched landscape with the addition of dead wood.

The presence of *Fomes fomentarius* plays a crucial role in forests in terms of nature conservation, food web dynamics, and decomposition processes: (i) As part of a group of indicator species, *Fomes fomentarius* has been used as an indicator for high conservation value and naturalness of forests (in Scandinavia in Jönsson et al., 2017; and in Central Europe in Müller et al., 2007 and Blaschke et al., 2009). *Fomes fomentarius* is especially suitable as an indicator from a practical point of view since it is relatively easy to survey (Heilmann-Clausen et al., 2015). (ii) *Fomes fomentarius* fruit bodies are very important as habitats for rare and common saproxylic and mycetophagous insects (Heilmann-Clausen et al., 2015; Stokland et al., 2012). A systematic study within Europe revealed more than 600 arthropod species living in decaying *Fomes fomentarius* sporocarps (Friess et al., 2019). (iii) Lastly, *Fomes fomentarius,* as a white-rot fungi, is equipped with the "full range of enzyme systems" necessary for degrading all wood components (i.e., cellulose, hemicellulose, and lignin) (Stokland et al., 2012).

Despite the importance of *Fomes fomentarius*, systematic experiments on how to enhance its occurrence in forests are lacking. Two key factors that affect fungal occupancy are microclimate and dead wood type. First, at the stand-scale, an opening in the canopy can affect the microclimate in several ways. An increase in 10% surface light after canopy treatments led to increases in temperature by 0.42 °C and vapour pressure deficit by 0.04 kPa compared to closed canopies in European beech-dominated forests (Thom et al., 2020). Canopy gaps were also observed to increase respiration rates and dead wood substrate temperature (Forrester et al., 2012). Microclimate has been observed to affect fungal composition. For example, higher temperature and radiation under canopy gaps affected fungal community composition in dead wood (Brabcová et al., 2022). Additionally, in the "harsher" microclimates created by canopy gaps, fungal fruit bodies with tougher flesh were more frequent (Krah et al., 2022). Furthermore, canopy openness was also shown to significantly affect fungal community composition (Krah et al., 2018). Second, dead wood type has been shown to affect fungal community composition and diversity. For example, in one study, logs were shown to support a larger number of fungal species compared to branches and stumps (Brazee et al., 2014). While some fungi may flourish in managed forests, where dead wood microhabitats can often be isolated and dominated by cut stumps and logging waste, many species can only be found in natural forests, where the dead wood is larger, older, and includes snags and logs (Heilmann-Clausen and Boddy, 2008; Nordén et al., 2020).

To test how the type of dead wood (i.e., log, snag, stump) as well as the microclimate, through variation in canopy cover, influence the occupancy and abundance of *Fomes fomentarius* at the stand- and dead wood object-scale, we set up an experiment in a random block design and manipulated European beech stands in patches of 50 m by 50 m by removing ca. 25% of the basal area applying the following treatments: 1) Only cut stumps remain, which we consider as the control, because this treatment represents the most common forest management practice in mature European beech forests during the thinning phase (e.g., Schall et al., 2017, Puettmann et al., 2015). 2) Logs and stumps remain, 3) snags remain, and 4) logs, stumps, and snags remain. On half of the stands, the canopy remained fairly closed after harvesting individual trees. On the other half, we created aggregated canopy gaps by cutting trees in groups of approximately 625 m^2. Altogether, we manipulated 40 forest stands located in five blocks. The investigated mature European beech forests were actively managed in the past (several decades ago), so that previous dead wood removal provided very little substrate for the fungus. At the stand-scale our research question was: What is the proportion of dead wood occupied (occupancy) in the alternative management treatments versus the control? At both the object- and stand-scale we asked: What is the mean abundance (measured as cover occupied by the fruit body in percent, termed "cover" hereafter) of *Fomes fomentarius* in the alternative management treatments versus the control?

2. Material and methods

2.1. Study area

The study took place in the Bavarian Forest National Park (BFNP) and in its close proximity. The BFNP has an area of ca. 25 000 ha and is located in south-east Germany on the border to the Czech Republic (48.9597° N, 13.3949° E). Together with the neighboring forested area in the Czech Republic, the region constitutes one of the largest forest landscapes in Central Europe (Bässler et al., 2009). Five locations (all sub-montane European beech forest areas) were studied. Four of these geographic blocks (hereafter "block") were within the management zone of the BFNP: GUG, JMH, KUH, TWF, and one block was located nearby in Thurmansbang (TUM). The forest stands where the research was conducted are dominated by European beech, with a low proportion of Norway spruce and other tree species. The forest originated from secondary succession and is characterized by low structural diversity (i.e., one canopy layer and low variation in tree age) (Thom et al., 2020). All stands are in a mature development stage and have similar basal areas, stand densities, and tree dimensions across study sites (Thom et al., 2020; Müller et al., 2023). The treatments were established in 2016 and comprise 40 stands, each 50 m by 50 m.

The treatments include two variables that were manipulated in a randomized block design: dead wood type and canopy (Fig. 1). We consistently removed ca. 25% of the basal area of vital trees (Thom et al., 2020). This resulted in approximately 24.5 m^3 ha^{-1} of logs and 3.3 m^2 ha^{-1} of snags across treatments which we left as dead wood (logs, snags, logs and snags; for further details, see Thom et al., 2020). This resulted in always the same approximate amounts of dead logs and snags irrespective of treatment. We left 1) only stumps and removed the complete trees (control, see Introduction), 2) we left only logs and their associated stumps, 3) we left only snags (trees cut below the crown remain), 4) we left logs and their associated stumps, and snags (hereafter referred to as "Mixed" stands). Tree crowns were always removed, so that deadwood amounts were comparable across all treatments. The individual-tree cuts

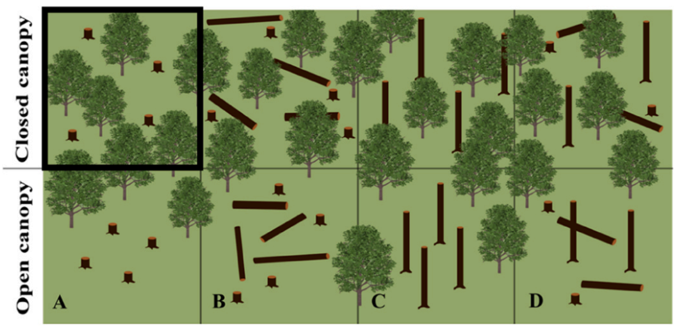

Fig. 1. Illustration of experimental stand treatments. Stands were 50 m by 50 m. Ca. 25% of the basal area was manipulated. The top row depicts stands with a closed canopy where dead wood is distributed across the stand. The bottom row depicts stands with an open canopy where dead wood is aggregated under the open canopy. In column A on the top (highlighted in bold) are stumps under a closed canopy (i.e., the control, resembling the dominant silviculture practice in temperate European beech forests), and open canopy. In column B are logs and their associated stumps, in column C are snags, and in column D are mixed dead wood types, including logs, their associated stumps, and snags.

allowed only little light to penetrate the canopy compared to the harvests in groups. We thus refer to the canopy treatments as "closed" and "open" hereafter. In the closed canopy treatment, trees were manipulated at a greater distance from one another to maintain a relatively closed canopy. This treatment resembles a single tree selection forest management strategy. In the open canopy treatment, trees were manipulated in close proximity to one another so as to create a large gap in the canopy. This treatment resembles either: group-selection cuts (Schall et al., 2017; Goßner et al., 2006) or a small-scale natural disturbance like local windthrow (Forrester et al., 2012). In the following, we use acronyms like "Open + Stumps", "Closed + Mixed", etc. for simplicity when referring to the treatments. In each of the five geographic blocks, eight unique treatments were assessed. The exception being that no Closed + Logs treatment was assessed in the block KUH, no Open + Stumps in TUM, and no Open + Stumps in KUH.

2.2. Fruit body survey

Stands were surveyed in autumn 2021 and 2022 during the main fruiting season by R.H. and P.K. All stumps, logs, and snags were assessed for occupancy (i.e., presence/absence) and percent cover occupied (i.e., abundance) of *Fomes fomentarius* fruit bodies (Fig. 2). Each object was divided into equally large sectors for the purpose of easy and reliable visual estimation of the percent cover occupied: logs and snags were assessed in three sectors along their length and stumps were assessed in their entirety because of their small size (Fig. 2). The radial area cut (i.e., the cut ends of a log, or the cut-off top of a stump or snag) was not considered. For the analysis, we compiled the data for each object. That is, occupancy reflects the existence (presence/absence) of *Fomes fomentarius* fruit bodies on an object irrespective of cover. Fruit body cover per object was calculated as a mean in percent based on the assessment of each sector. Therefore, the object was the elementary unit for all analyses presented in this study.

2.3. Data analysis

To address what proportion of dead wood objects was occupied by *Fomes fomentarius* fruit bodies (occupancy) at the stand-scale, we used a Generalized Linear Mixed-effects Model applying the *glmmTMB* package in R (using the "beta" family and "logit" link; hereafter, "glmm") (Brooks et al., 2017). The proportion of objects per stand occupied by *Fomes fomentarius* was the response variable, treatment was a fixed effect, and block was the random effect. We used the Closed + Stumps treatment as the control group as this is in line with our research questions (see Introduction). To assess the mean cover by *Fomes fomentarius* fruit bodies in the forest management treatments at the stand-scale, we used again a glmm with mean stand-scale cover as the response variable, treatment as the fixed effect, and block as the random effect. Again, we used the Closed + Stumps treatment as the control group. In this case, the response variable was defined as the mean area in percent across dead wood objects at the stand-scale that were occupied by *Fomes fomentarius* fruit bodies. It is hence a relative abundance value which accounts for differences in resource availability depending on dead wood type. Finally, to analyze the cover of *Fomes fomentarius* fruit bodies at the object-scale on logs, snags, and stumps in relation to the treatments, we used a glmm with object-scale cover as the response variable, dead wood type and canopy treatment as fixed effects and stand within block as the nested random effects. We used the Closed + Stumps treatment as the control group.

For deeper insights, we applied post hoc Tukey tests and tested for all pairwise differences among treatments. Further details and the results from the post hoc tests can be found in Appendices A.1-A.3. The *tab_model* function was used for computing marginal R^2 values. All statistical analyses were performed in R version 4.2.1 (R Core Team, 2022) and images were created using the package *ggplot2* (Wickham, 2016).

3. Results

Fomes fomentarius fruit bodies were present in 91.9% of all stands. Moreover, *Fomes fomentarius* fruit bodies were present on 33.3% of the 1186 individual objects investigated. Snags under closed canopies had the highest mean *Fomes fomentarius* fruit body cover, whereas logs in

Table 1
Mean object-scale *Fomes fomentarius* fruit body cover (%) and percent of objects where *Fomes fomentarius* fruit bodies were present, grouped by dead wood type and canopy treatment.

	Mean object-scale *F. fomentarius* cover (%) Dead wood type			Objects occupied by *Fomes fomentarius* (%)		
Canopy	Logs	Snags	Stumps	Logs	Snags	Stumps
Open	14.28	16.84	9.66	62.64	55.48	9.52
Closed	13.99	23.13	14.52	50	48.32	9.47

Fig. 2. Examples of all three dead wood substrate types with *Fomes fomentarius* fruit bodies present.

open canopy stands had the greatest proportion of *Fomes fomentarius* fruit bodies (Table 1).

3.1. Stand-scale proportion of dead wood occupied by Fomes fomentarius fruit bodies

We found significantly higher proportions of dead wood occupied by *Fomes fomentarius* after alternative treatments, except for Open + Stumps, compared to the control (i.e., Closed + Stumps) (Table 2, Fig. 3). The coefficient of determination, given as marginal R^2 was 0.87. The results of the post hoc test can be found in Appendix A.1.

3.2. Stand-scale cover of Fomes fomentarius fruit bodies on dead wood

The higher cover of *Fomes fomentarius* fruit bodies observed on Closed + Snags stands was statistically significant when compared to Closed + Stumps (glmmTMB: z = 2.68, p-value: 0.008) (Table 3, Fig. 4). The marginal R^2 was 0.57. The results of the post hoc test can be found in Appendix A.2.

3.3. Object-scale cover of Fomes fomentarius fruit bodies on dead wood

We tested the effect of dead wood type and canopy on the cover of *Fomes fomentarius,* with "stand in block" as nested random effects using Closed + Stumps as the control (Table 4, Fig. 5). The higher cover of *Fomes fomentarius* on Closed + Snags stands was statistically significant when compared to Closed + Stumps (glmmTMB: z = 2.14, p = 0.033). The marginal R^2 was 0.11. The results of the post hoc test can be found in Appendix A.3.

4. Discussion

The aim of this study was to ascertain how dead wood type in combination with canopy provided by different forest management strategies affect the occupancy and cover of *Fomes fomentarius*. We found that dead wood enrichment of logs and snags increased the occupancy and that snags increased the mean cover of *Fomes fomentarius* fruit bodies significantly compared to if only cut stumps were left underneath closed canopies, which is still the dominant silvicultural practice in European beech forests.

4.1. Fomes fomentarius fruit body occurrence in different forest management treatments

Forest management treatments may cause differences in *Fomes fomentarius* fruit body occupancy, specifically, the proportion of objects colonized in a forest stand. We found that an enrichment of dead wood with logs and snags did indeed increase the occupancy. Consequently, leaving only cut stumps after logging resulted in a significantly lower proportion of objects occupied. The created availability of resources might explain this finding. (i) A higher availability of resources, specifically, higher amounts of large logs and snags, increases the chance of colonization by *Fomes fomentarius* via dispersed spores from the

Table 2
Generalized Linear Mixed-effects Model of the effect of canopy openness and dead wood type on the occupancy of *Fomes fomentarius* fruit bodies on the stand-scale. The reference group was Closed + Stumps (control).

	Estimate	Std. error	Effect size (z)	Pr (>|z|)
Open + Stumps	-0.14	0.64	-0.22	0.828
Closed + Logs + Stumps	2.01	0.52	3.87	< 0.001
Open + Logs + Stumps	2.25	0.50	4.53	< 0.001
Closed + Snags	2.50	0.49	5.06	< 0.001
Open + Snags	2.75	0.51	5.38	< 0.001
Closed + Mixed	2.24	0.49	4.53	< 0.001
Open + Mixed	2.80	0.49	5.65	< 0.001

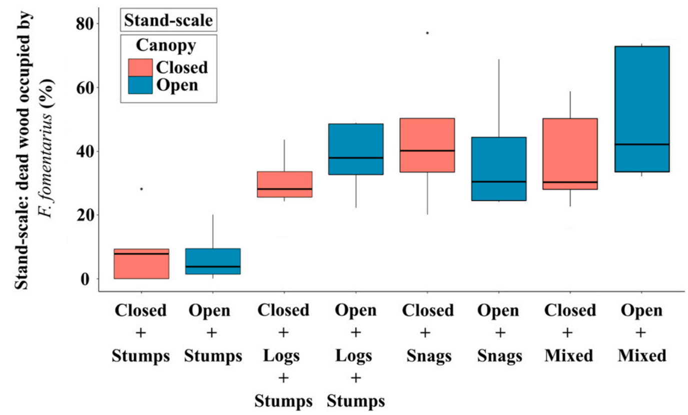

Fig. 3. Raw data showing the proportion of dead wood occupied by *Fomes fomentarius* fruit bodies at the stand-scale grouped by treatment (i.e., canopy and dead wood type).

Table 3
Generalized Linear Mixed-effects Model of the effect of canopy openness and dead wood type on the mean cover of *Fomes fomentarius* fruit bodies on the stand-scale. The reference group was Closed + Stumps.

	Estimate	Std. error	Effect size (z)	Pr (>|z|)
Open + Stumps	-0.66	0.44	-1.51	0.131
Closed + Logs + Stumps	-0.05	0.36	-0.14	0.886
Open + Logs + Stumps	0.03	0.34	0.08	0.935
Closed + Snags	0.86	0.32	2.68	0.008
Open + Snags	0.26	0.35	0.75	0.452
Closed + Mixed	0.25	0.34	0.74	0.462
Open + Mixed	0.10	0.34	0.28	0.780

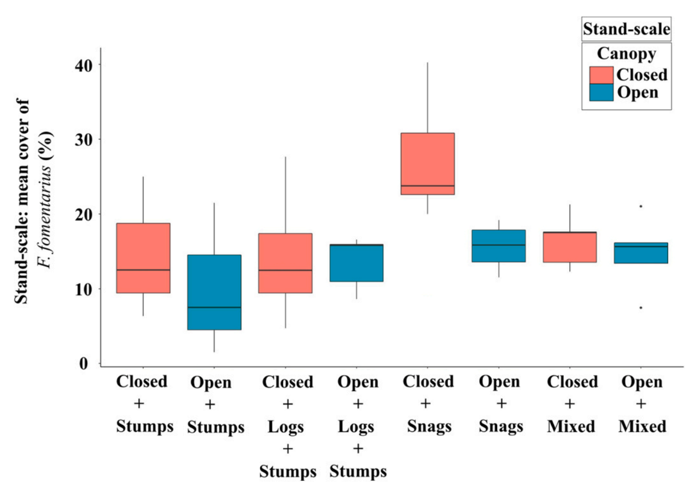

Fig. 4. Raw values of the mean stand-scale cover of *Fomes fomentarius* fruit bodies grouped by treatment.

Table 4
Generalized Linear Mixed-effects Model of the effect of canopy openness and dead wood type on the mean cover of *Fomes fomentarius* fruit bodies on the object-scale. The reference group was Closed + Stumps.

	Estimate	Std. error	Effect size (z)	Pr (>|z|)
Open + Stumps	-0.51	0.29	-1.80	0.072
Closed + Logs	0.03	0.23	0.14	0.889
Open + Logs	-0.05	0.23	-0.21	0.836
Closed + Snags	0.488	0.23	2.14	0.033
Open + Snags	0.149	0.23	0.65	0.519

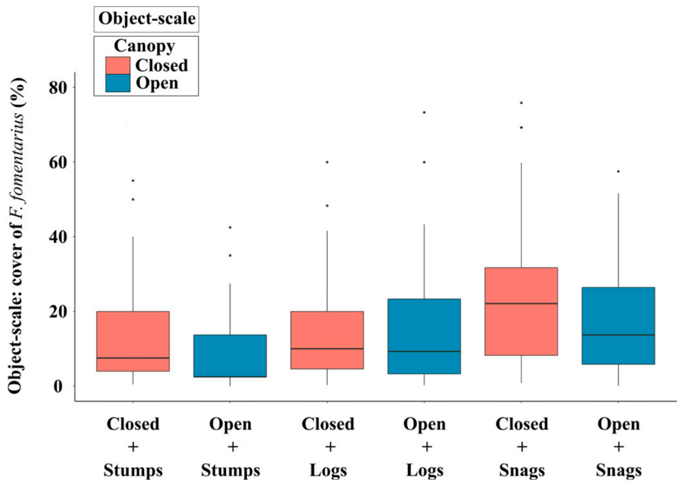

Fig. 5. Raw values of the object-scale cover of *Fomes fomentarius* fruit bodies grouped by dead wood type and canopy.

surroundings (i.e., abundance-area relationship based on island biogeography theory, MacArthur and Wilson, 2001). (ii) *Fomes fomentarius* is known as a species that can establish itself in living trees as an endophyte (Baum et al., 2003; Parfitt et al., 2010). Furthermore, old, and senescent but still living trees are often characterized by *Fomes fomentarius* fruit bodies, underpinning the fungus' parasitic-decaying continuum lifestyle (Lange, 1992). Therefore, large substrates like logs and snags might harbor larger sizes of endophytic mycelia that increase the probability of fruiting (Piętka et al., 2019). Moreover, larger substrates have more heterogenous environmental characteristics (Caruso et al., 2008). Increased environmental variability within a substrate caused by size might increase the chance of triggering fruiting through a higher probability of suitable fruiting cues. (iii) Closely related to the above points, we learned from previous studies that a minimum size of mycelium is necessary to produce fruit bodies (Bässler et al., 2014). The larger the fruit bodies a species produces, the larger the minimum size mycelium that must be present (Bässler et al., 2015). Polypores like *Fomes fomentarius* produce large fruit bodies and hence a large minimum mycelium size is needed. We would not expect that the amount of resource that stumps provide is generally too little for the production of *Fomes fomentarius* fruit bodies. However, competition among species for space and resources within dead wood is very pronounced (Woodward and Boddy, 2008). If many other species coexist within a stump, the effective size of *Fomes fomentarius* mycelia might be limited and hence, fruit body production is limited. (iv) Another explanation could be that specific environmental constraints exist inside stumps that limit the development of *Fomes fomentarius*. Due to their smaller size, the microclimate of stumps might be less buffered than inside large logs and snags. Higher microclimatic variability and extremes might limit *Fomes fomentarius*. However, several studies showed that stumps decay faster than logs and snags (Yatskov et al., 2003; Tobin et al., 2007; Shorohova and Kapitsa, 2014), indicating that the stump environment is benign and fungal metabolism is not limited. More studies are needed to characterize the environmental conditions and the mycelial size of *Fomes fomentarius* and co-occurring species in different dead wood types. Even though mechanisms remain hidden in our study, an enrichment of dead wood increases resource availability and boosts *Fomes fomentarius* fruit bodies and related processes.

4.2. The importance of snags for *Fomes fomentarius* fruit body cover

Our models showed that *Fomes fomentarius* fruit body cover is significantly higher on snags than on stumps in closed conditions at the stand- and object-scale. However, this was not supported by the results of the post hoc tests (Appendix Tables A.2 and A.3). This could be due to the relatively high number of factor levels and the subsequent statistical penalty when accounting for multiple comparisons. Note that the raw values of the mean cover of *Fomes fomentarius* fruit bodies at the stand-scale of Closed + Snags versus Closed + Stumps differ substantially (i.e., interquartile ranges are not overlapping, Fig. 4). Nevertheless, we cautiously interpret that similar mechanisms as described above for occupancy might explain the observed differences in mean cover between the snag treatment and the control (stumps), that is, differences in resource availability (e.g., colonization could occur at different localities within the object thus increasing mean cover), environmental conditions, and biotic interactions (e.g., competition).

4.3. Occupancy and mean cover of *Fomes fomentarius* fruit bodies under different canopies

Our model revealed significantly higher *Fomes fomentarius* fruit body occupancy after dead wood enrichment irrespective of canopy treatment at the stand-scale. Further, in all treatments (except for Closed + Snags) *Fomes fomentarius* cover was not significantly different from the closed control treatment at the object- and stand-scale. This indicates that *Fomes fomentarius* fruit bodies can develop under open and closed canopies. Intact forest canopies are better able to buffer weather extremes than forests with a disturbed canopy (Thom et al., 2020; Brabcová et al., 2022). However, based on our findings, it seems that *Fomes fomentarius* fruit bodies can cope with harsher microclimates under disturbed canopies. One explanation might be that *Fomes fomentarius* produces tough perennial fruit bodies that develop also under hot and dry conditions (Krah et al., 2022).

5. Conclusions

Fomes fomentarius is a key decomposer in European beech forests and its presence is additionally important in the context of nature conservation, food web dynamics, as well as for providing habitat for many saproxylic species. Our study shows that the enrichment of snags and logs in forests boosts *Fomes fomentarius* fruit body occupancy. Of the dead wood types studied, we recommend particularly the enrichment of snags under closed canopies during logging operations. However, to attain overall saproxylic diversity one should not only focus on promoting the conditions relevant for a single fungus species. We, therefore, recommend additionally considering diverse microclimatic conditions and dead wood substrate types in forest management at the landscape scale.

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CRediT authorship contribution statement

Bronwyn Lira Dyson: Methodology, Formal analysis, Writing – original draft, Visualization. **Rhea Herpel**: Investigation, Data curation. **Peter Karasch**: Investigation, Data curation, Writing – review & editing. **Jörg Müller**: Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Project administration. **Dominik Thom**: Conceptualization, Methodology, Formal analysis. **Claus Bässler**: Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision, Funding acquisition, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendices

Table A.1
A post hoc Tukey test of pairwise comparisons of the effect of treatment on stand-scale proportion of *Fomes fomentarius* with block as random effect. The data was normally distributed. We used the *emmeans* package (Length, 2023) and *pairs* function to account for multiple comparisons. Significance effects are indicated by asterisks, where '**' is $p < 0.01$, and '***' to $p < 0.001$.

Treatment 1	Treatment 2	Effect size (z)
Open + Stumps	Closed + Logs + Stumps	-3.545 * *
Open + Stumps	Open + Logs + Stumps	-4.150 * **
Open + Stumps	Closed + Snags	-4.579 * **
Open + Stumps	Open + Snags	-4.770 * *
Open + Stumps	Closed + Mixed	-4.139 * **
Open + Stumps	Open + Mixed	-5.077 * **
Open + Stumps	Closed + Stumps	-0.218
Closed + Logs + Stumps	Open + Logs + Stumps	-0.556
Closed + Logs + Stumps	Closed + Snags	-1.171
Closed + Logs + Stumps	Open + Snags	-0.707
Closed + Logs + Stumps	Closed + Mixed	-0.547
Closed + Logs + Stumps	Open + Mixed	-1.894
Closed + Logs + Stumps	Closed + Stumps	3.873 * *
Open + Logs + Stumps	Closed + Snags	-0.661
Open + Logs + Stumps	Open + Snags	-1.238
Open + Logs + Stumps	Closed + Mixed	0.013
Open + Logs + Stumps	Open + Mixed	-1.443
Open + Logs + Stumps	Closed + Stumps	4.529 * **
Closed + Snags	Open + Snags	0.622
Closed + Snags	Closed + Mixed	0.678
Closed + Snags	Open + Mixed	-0.790
Closed + Snags	Closed + Stumps	5.062 * **
Open + Snags	Closed + Mixed	1.257
Open + Snags	Open + Mixed	-0.123
Open + Snags	Closed + Stumps	5.377 * **
Closed + Mixed	Open + Mixed	-1.463
Closed + Mixed	Closed + Stumps	4.530 * **
Open + Mixed	Closed + Stumps	5.653 * **

Table A.2
A post hoc Tukey test of pairwise comparisons of the effect of treatment on abundance of *Fomes fomentarius* with block as random effect. The data was normally distributed. We used the *emmeans* package (Length, 2023) and *pairs* function to account for multiple comparisons. Significant effects are indicated by asterisks, where '*' is $p < 0.05$, '**' is $p < 0.01$.

Treatment 1	Treatment 2	Effect size (z)
Open + Stumps	Closed + Logs + Stumps	-1.457
Open + Stumps	Open + Logs + Stumps	-1.720
Open + Stumps	Closed + Snags	-3.995 * *
Open + Stumps	Open + Snags	-2.281
Open + Stumps	Closed + Mixed	-2.308
Open + Stumps	Open + Mixed	-1.899
Open + Stumps	Closed + Stumps	-1.510
Closed + Logs + Stumps	Open + Logs + Stumps	-0.251
Closed + Logs + Stumps	Closed + Snags	-3.101 *
Closed + Logs + Stumps	Open + Snags	-0.971
Closed + Logs + Stumps	Closed + Mixed	-0.965
Closed + Logs + Stumps	Open + Mixed	-0.466
Closed + Logs + Stumps	Closed + Stumps	-0.143
Open + Logs + Stumps	Closed + Snags	-3.088 *
Open + Logs + Stumps	Open + Snags	-0.777
Open + Logs + Stumps	Closed + Mixed	-0.764
Open + Logs + Stumps	Open + Mixed	-0.229
Open + Logs + Stumps	Closed + Stumps	0.082
Closed + Snags	Open + Snags	2.160
Closed + Snags	Closed + Mixed	2.365
Closed + Snags	Open + Mixed	2.875
Closed + Snags	Closed + Stumps	2.676
Open + Snags	Closed + Mixed	0.054
Open + Snags	Open + Mixed	0.560

(*continued on next page*)

Table A.2 (*continued*)

Treatment 1	Treatment 2	Effect size (z)
Open + Snags	Closed + Stumps	0.753
Closed + Mixed	Open + Mixed	0.536
Closed + Mixed	Closed + Stumps	0.736
Open + Mixed	Closed + Stumps	0.279

Table A.3
A post hoc Tukey test of pairwise comparisons of the effect of treatment on abundance of *Fomes fomentarius* with stand in block as nested random effects. We used the *emmeans* package (Length, 2023) and *pairs* function to account for multiple comparisons. As the data was not normally distributed, we conducted the post hoc Tukey test on the log10 transformed data after running a linear mixed-effects model (Bates et al., 2015). Significant effects are indicated by asterisks, where '* ' is $p < 0.05$ and '* ** ' to $p < 0.001$.

Treatment 1	Treatment 2	Effect size (z)
Open + Stumps	Closed + Logs + Stumps	-3.218 *
Open + Stumps	Open + Logs + Stumps	-3.118 *
Open + Stumps	Closed + Snags	-4.785 * **
Open + Stumps	Open + Snags	-4.015 * *
Open + Stumps	Closed + Stumps	-2.287
Closed + Logs + Stumps	Open + Logs + Stumps	0.745
Closed + Logs + Stumps	Closed + Snags	-2.044
Closed + Logs + Stumps	Open + Snags	-0.716
Closed + Logs + Stumps	Closed + Stumps	0.430
Open + Logs + Stumps	Closed + Snags	-2.804
Open + Logs + Stumps	Open + Snags	-1.667
Open + Logs + Stumps	Closed + Stumps	-0.133
Closed + Snags	Open + Snags	1.280
Closed + Snags	Closed + Stumps	1.908
Open + Snags	Closed + Stumps	0.963

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