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Incipient decay in beech (*Fagus sylvatica* L.) and linden (*Tilia cordata* Mill.): An interspecific static and dynamic material analysis

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ABSTRACT

With increasing awareness of the ecological value of trees in urban areas, there is a growing need to preserve mature specimens often colonised by wood-decay fungi. Nonetheless, cases of stem collapse or uprooting of such trees under adverse weather conditions remain a significant issue requiring further investigation. Depending on the decay type and the wood structure of the host tree, different combinations of wood-decaying fungi and host species can have varying impacts on the mechanical and vibroacoustic properties of green wood. This study compares the physical and mechanical properties of green European beech (*Fagus sylvatica* L.) and small-leaved linden (*Tilia cordata* Mill.) artificially exposed to *Fomes fomentarius* (L.) Fr. and *Kretzschmaria deusta* (Hoff.) P.M. D. Martin after different exposure periods. Mass loss (*ML*) caused by both fungi differed according to the wood species. A statistically significant difference between the two fungal species was observed in beech wood, but not in linden. Significant differences in the modulus of rupture (*MOR*) and dynamic bending modulus of elasticity (*MOED*) were observed among the fungus-wood combinations, also depending on the exposure time. The relationships between *ML* and *MOR* varied according to the fungal species, where at the same *ML* values, *K. deusta* caused a higher *MOR* loss in both wood species. Strong relationships between *MOED* and *MOR* were demonstrated for all fungus-wood combinations, without significant differences related to the decay type. The *MOED* is a reliable parameter for predicting *MOR* loss even at incipient degradation stages, irrespective of the type of decay. The presented results can lead to better prediction of the impact of fungal colonization on standing trees and improve non-destructive methods used for tree stability assessment.

1. Introduction

Wood degradation in standing trees can be approached in two different ways: on one side, fungal colonization of mature and veteran trees is a natural physiological process aimed at recycling the unfunctional wood material (e.g., heartwood) (Fukasawa, 2021; Rayner and Boddy, 1988). Furthermore, degraded wood provides resources for a variety of living organisms (Ódor and Van Hees, 2004). In some cases, standing trees are even artificially inoculated with specific fungal strains to enhance their ecological value and potential (Filip et al., 2011; Wainhouse and Boddy, 2022). On the other hand, fungal deterioration can cause significant changes in the material properties of colonised wood (Rypáček, 1957; Xu et al., 2019), even at an incipient stage of decay (Curling et al., 2002; Fackler et al., 2010). Under adverse weather conditions, these changes can lead to potential structural collapses of trees, such as stem breakage or uprooting (Kobza et al., 2022; Soge et al., 2021). This risk is even heightened in urban environments, where stressed living trees struggle to adequately react to fungal colonisation due to a lack of energy (carbon) reserves (Wiley, 2020). Wood-decaying fungi, according to their enzymatic activity and decay patterns, can be classified into three different categories: brown, white, and soft rot fungi (Rayner and Boddy, 1988). White-rot fungi (*WRF*) cause the degradation of all components of the lignified cell wall (Messner et al., 2003). According to microscopic analyses, white rot can be distinguished into two main groups (Blanchette, 1984; Liese, 1970): simultaneous white rot, where all cell wall components are uniformly degraded over time, and selective delignification (or sequential white rot), where, at least in the early decay stage, lignin and hemicellulose are preferentially degraded (Daniel, 2016; Schmidt, 2006). Soft-rot fungi (*SRF*) primarily belong to the division Ascomycota, although different authors have demonstrated that various basidiomycetes causing white rot can exhibit decay patterns similar to *SRF* (Bari et al., 2020; Cristini et al., 2023).

Unlike brown rot fungi and *WRF*, which cause decay from the cell lumina, degrading the surrounding cell-wall components eccentrically

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(Daniel, 2016; Schwarze et al., 2004), *SRF* grow mainly inside the lignified cell wall, producing chains of cavities within the S2 layer. The continuous enlargement of these cavities, together with the formation of new ones, leads to the total degradation of the secondary wall (soft rot type I) (Schmidt, 2006). Nevertheless, *SRF* can also deteriorate the cell wall by extending their degradation from the cell lumen to the middle lamella (soft rot type II) (Hale and Eaton, 1985; Nghi et al., 2012). Considering that most trees in the urban environment of central Europe are hardwoods (Roloff et al., 2018), this article focuses on the effect of fungal degradation caused by *WRF Fomes fomentarius* (L.) Fr. (*F. fomentarius*) and *SRF Kretzschmaria deusta* (Hoff.) P.M.D. Martin (*K. deusta*), which typically colonise (Schwarze et al., 2004). *F. fomentarius* is a *WRF* causing simultaneous rot of wood from various species, including European beech and small-leaved linden, making it one of their primary decomposers (Větrovský et al., 2011). This fungus is well known for typically causing heart rot in standing trees, colonising its host through mechanical wounds or from a previous latent endophytic phase (Baum et al., 2003; Boddy, 2021). In trees at an advanced colonisation stage, often causes fractures with an extremely brittle structure (Schwarze et al., 2004). Different studies have shown that *F. fomentarius* can cause significant mass and strength loss in beech wood after relatively short incubation periods (Bari et al., 2021; Cristini et al., 2023). However, the impact of its enzymatic activity on the anatomical, physical, and mechanical properties of wood from the initial stages of decay remains unexplored. *K. deusta* is known as an *SRF* causing heart rot in various tree species, including beech, linden, and maple (Guglielmo et al., 2012; Latałowa et al., 2013; Schwarze et al., 2004). A study by Cordin et al. (2021) suggested that colonisation by *K. deusta* could compromise the long-term conservation of ancient beech trees, potentially leading to their mechanical failure. Deflorio et al. (2008) demonstrated that artificial inoculation of beech trees with *K. deusta* results in a significant decrease in stress-wave velocity, indicative of substantial strength loss. Moreover, Cristini et al. (2022) found a strong correlation between dynamic bending modulus of elasticity (*MOED*) and strength loss in green beech wood after 12 weeks of fungal exposure. Nevertheless, Schwarze et al. (1995) observed that the initial stage of lignified cell wall degradation led to strength loss without significant changes in measured stress-wave velocity, which could influence the outcomes of acoustic tomography assessments (Schwarze et al., 2004). To gain a more comprehensive understanding of *K. deusta*'s intricate effects on the material properties of different wood species across various degradation stages, further research is necessary. The two fungal species selected for this study are known to colonise two common tree species in Central Europe: European beech (beech) and small-leaved linden (linden) (Klein et al., 2016). These species were chosen to represent two distinct groups of diffuse-porous wood, one with lower (linden) and the other with higher (beech) wood density (Kretschmann, 2010; Niklas and Spatz, 2010). Owing to the greater precision of vibro-acoustic non-destructive methods in evaluating the mechanical properties of decayed wood, compared to mass loss (*ML*) assessments, several researchers have explored the relationship between static and dynamic mechanical parameters (Machek et al., 2001; Schwarze et al., 1995; Stanciu et al., 2020; Yang et al., 2017). However, most of these studies, have been performed on softwood species artificially inoculated with fungal strains typically associated with construction timber (Frühwald et al., 2012). Furthermore, many of these investigations focus on properties at a moisture content (*MC*) below the fibre saturation point (*FSP*), which is not representative of the conditions in standing trees, where the *MC* is usually above the *FSP* (Dahlen et al., 2020; Tomczak et al., 2018). Our study offers a new insight into the relationship between static and dynamic mechanical properties of green wood from two species across different stages of decay, induced by two wood-decay fungi often colonising standing trees. These insights have the potential to deepen our comprehension of how these two fungal species impact the stability of standing trees and refine predictions regarding the likelihood of tree collapse.

To achieve the above-mentioned objectives, the following hypotheses were formulated:

- The decay rate in each wood species will differ according to the fungal strain used for artificial exposure.
- The impact of decay by each fungal species will differ according to the exposed wood species.
- The relationships between mass loss (ML) and mechanical/vibroacoustic properties will differ according to the type of decay.

2. Materials and methods

2.1. Samples' preparation

All samples were crafted in August 2022 from naturally dried boards of beech and linden wood. The beech wood was sourced from the University Forest Enterprise Masarykův les Křtiny (CZ), while the linden wood came from freshly felled trees in a street in Brno (CZ) in 2021, necessitated by construction activities. The trees selected for sample crafting exhibited no visible signs of fungal colonisation. The crafting process exclusively utilised intact sapwood. From these boards, small specially orthotropic bending samples measuring 7 ×7 x 100 mm were prepared for both species, following the methodology outlined by Cristini et al. (2022). In total, 200 samples for each wood species were prepared for fungal exposure, (12 specimens per week of exposure for each fungus + an additional 8 samples per wood species serving as control groups). For the testing of intact samples (reference), another 30 specimens for each species were prepared. The oven-dry mass of the samples prior to fungal exposure was determined by drying them in a kiln at 103°C until they reached steady conditions. Before vibro-acoustic measurements and the inoculation of the samples, a *MC* above *FSP* was achieved through vacuum impregnation with demineralised water (20 kPa, 30 seconds to 3 minutes). The impregnation time was adjusted according to the wood species. Throughout the impregnation process, a similar mass of water (approximately 2 g) was absorbed by the specimens of both species. Due to the lower density of linden wood, the absolute *MC* after impregnation (MC_{mean} = 98 %) was higher than that of beech wood (MC_{mean} = 68 %). The precise *MC* following sterilisation remained unknown; however, based on previous tests, the sterilisation process resulted in *MC* reductions of approximately 10–15 % for beech and 15–25 % for linden specimens.

2.2. Artificial fungal exposure

2.2.1. Fungal cultures and flasks preparation

The *F. fomentarius* strain was obtained from a basidiocarp growing on a beech tree within the forest. The *K. deusta* strain was isolated from the wood of a mature standing beech tree situated at the forest's edge. Both specimens were collected from trees on the grounds of the University Forest Enterprise Masarykův les Křtiny (CZ). Prior to flasks inoculation, cultures from both fungi were cultivated on small beech and linden wood blocks in Petri dishes to stimulate their enzymatic activity.

After this period, small pieces of the inoculated wood blocks were utilised to prepare Petri dishes for the inoculation of culture flasks. Kolle culture flasks (400 ml) served for the fungal exposure of the bending samples. Each flask contained 70 ml of sterile malt extract agar base (malt extract = 30 g/l; mycological peptone = 5 g/l; agar = 15 g/l; with a final medium concentration of 5 %). Following a two-week incubation at 22 °C and 70 % relative humidity, the surface of the medium was entirely covered by mycelium, ready for sample insertion.

2.2.2. Fungal exposure of bending samples

Following water impregnation and the initial vibro-acoustic evaluation, all specimens were sterilised using steam (10 minutes, 120°C) and positioned on their radial faces in accordance with the methodology outlined by Cristini et al. (2022). Each Kolle flask contained four

bending specimens (Fig. 1). Over the next eight weeks, samples were periodically extracted at weekly intervals from the fungal environment for vibro-acoustic and static mechanical testing. At the final measurement session, all control specimens (8 per species, consisting of 4 Kolle flasks without fungal cultures) were retrieved and oven-dried. No mass loss was recorded for the control samples.

2.3. Vibro-acoustic testing

The vibro-acoustic evaluation was performed on all samples both before and after fungal exposure. The resonance frequency technique was employed to determine the dynamic bending modulus of elasticity in the tangential loading direction (*MOED*), which was calculated according to the following equation:

$$MOED = \left(\frac{2f_t}{2.25\pi}\right)^2 \frac{ml^3}{I_t} \quad (1)$$

where f is the resonant frequency of the first bending mode, m is the sample mass, l is the sample length, and I is the moment of inertia. Oscillations were induced by striking the centre of top side with a mallet. Vibrations in the longitudinal–tangential bending modes were detected using a Doppler laser vibrometer (PDV-100, Polytec Inc., CA, USA) (Fig. 2a). The entire process of vibro-acoustic testing, including signal processing and subsequent calculations, was done in MATLAB® (The MathWorks, Inc., Natick, MA, USA), following the methodology described by Cristini et al. (2022).

2.4. Mechanical testing

Static three-point bending tests in a tangential direction were carried out on a universal testing machine (Tinius Olsen, Redhill, UK) (Fig. 2b). The modulus of rupture (*MOR*) was calculated as the bending stress according to the following equation:

$$MOR = \frac{3Fl_0}{2bh^2} \quad (2)$$

Where F is the maximal applied force, l_0 is the distance between the two supports (12 times the sample's height), and b, h are the width and the height of the specimen's cross-section. The data were processed using MATLAB®. After testing, all samples were dried in a kiln at 103 °C and weighed after approaching steady conditions to obtain their dry weight. The *ML*, *MC*, and green density (ρ_w) were calculated from sample dimensions at green conditions and dry/wet (before and after degradation) masses, according to the following equations:

$$ML = \frac{mass_{id} - mass_{dd}}{mass_{id}} * 100 \quad (3)$$

$$MC = \frac{mass_w - mass_d}{mass_d} * 100 \quad (4)$$

$$\rho_w = \frac{mass_w}{v} \quad (5)$$

Where $mass_{id}$ is the dry mass of the intact samples before fungal exposure, $mass_{dd}$ is the dry mass of the samples after fungal exposure, $mass_d$ is the dried mass and $mass_w$ is the wet mass.

2.5. Scanning Electron Microscopy (SEM) assessment

A scanning electron microscope was used to conduct microscopy analysis (TESCAN, Brno, CZ). Small samples (4 ×4×4 mm) were sectioned from 18 different specimens (1 sample for each wood-fungus combination for exposure groups 2, 4, 6 and 8 weeks and 1 intact sample for each wood species). The samples were chosen based on whether their ML was the closest to the average one for each sample group. All the small samples were prepared from the middle part of the length of each selected bending specimen, avoiding the fractured and deformed zone caused by static testing. Sample preparation and microscopy setup are described in detail by Cristini et al. (2022).

2.6. Statistical analysis

Statistical analyses of the assessed parameters were performed in MATLAB®, using Spearman's correlation coefficient (*Sc*), coefficient of variation (*CV*), and polynomial curve fitting. Due to the considerable variability of the measured data, arising both from the wood as a natural material and the significant variability induced by fungal degradation, the significance level for Kruskal-Wallis and multiple comparison tests was set to 0.001, a common threshold in wood science research (van Duong and Matsumura 2018). The one-sample Kolmogorov-Smirnov

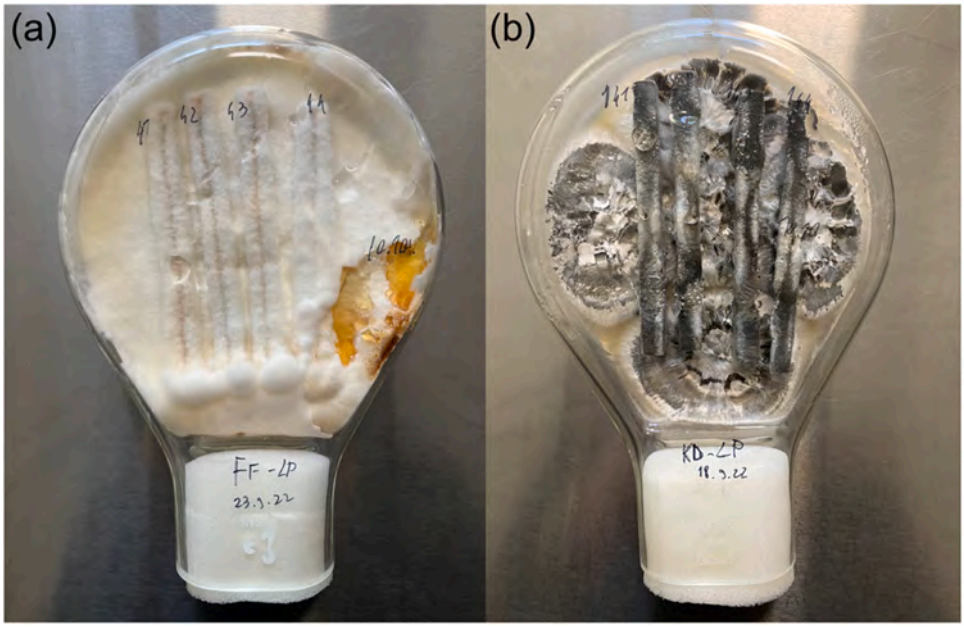

Fig. 1. Small bending samples during fungal exposure to *F. fomentarius* (a) and *K. deusta* (b) in Kolle culture flasks.

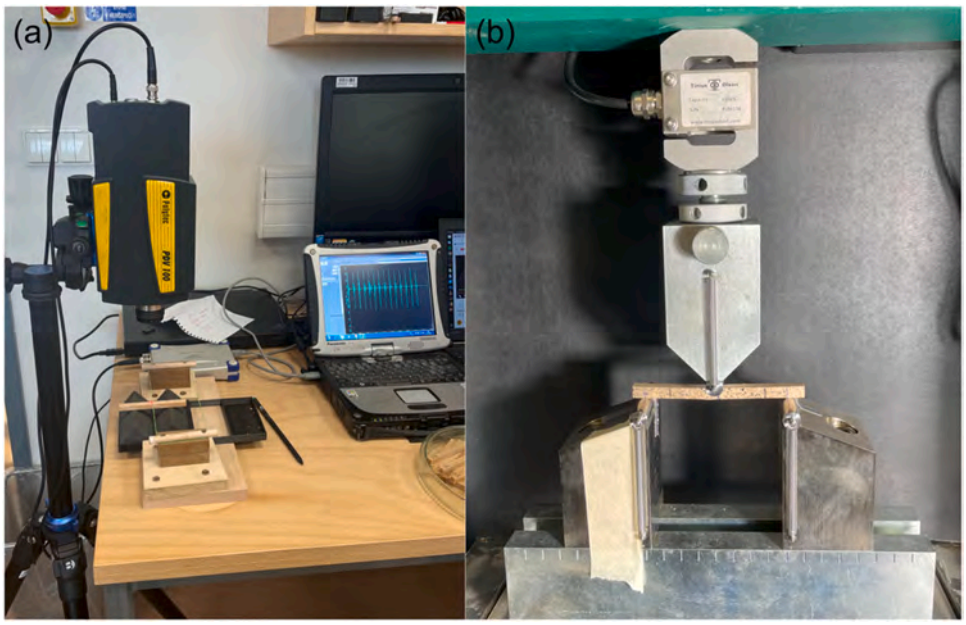

Fig. 2. vibro-acoustic testing of small bending samples with the Doppler's laser vibrometer (a), and static three-point bending mechanical testing with a universal testing machine (b).

test was used to assess the distribution of the data.

3. Results

3.1. Comparison of ML and decay patterns between wood and fungal species

As illustrated in Fig. 3, there is a significant difference in *ML* of beech samples caused by the two wood decay fungi (Fig. 3a). Excluding the first week of exposure, a statistically significant difference between *F. fomentarius* and *K. deusta* on beech wood was proved ($p < 0.001$). This observation holds true for a comprehensive comparison of the more advanced decay stages (average *ML* values from the last three weeks of exposure: 42.72 % for *F. fomentarius* and 17.82 % for *K. deusta*). However, as depicted in Fig. 3b, *ML* values measured on linden samples affected by both fungi appear more similar.

Contrary to beech wood, excluding the first week of exposure, no statistically significant difference in linden *ML* caused by the two fungi was confirmed ($p > 0.001$). For linden, the mean *ML* values from the last three weeks of exposure are 30.78 % for *F. fomentarius* and 27.45 % for *K. deusta*. Generally, even when considering the variability of degraded wood properties, the ML variability for each group was moderate (*CV* range = 5.8 % - 34.7 %). This observation also applies to the late-stage groups representing the last three weeks of exposure, with a *CV* range of 11.04 % - 21.35 %.

Figs. 4 and 5 depict the decay patterns of both fungi on beech (Fig. 4) and linden wood (Fig. 5). From the SEM scans, it is evident that *F. fomentarius* induces degradation patterns in both wood species typical of simultaneous white-rot fungi. A progressive colonisation of the lumina of libriform fibres led to an outward degradation of the cell wall, advancing to decay stages where even the compound middle lamella is deteriorated (Figs. 4e and 5e).

K. deusta induced in both wood species a progressive type I soft rot, characteristic of this fungus (Levy, 1966). After two weeks of exposure, small cavities began to form in the S2 layer of libriform fibres in both beech (Fig. 4f) and linden wood (Fig. 5f). In the next phases, the presence of cavities became more common, and they started to connect by increasing their diameters (Figs. 4g,h and 5g,h). After 8 weeks of exposure, both wood species exhibited decay patterns indicative of advanced soft rot, where the merging of different cavities led to the almost complete degradation of the secondary cell wall while leaving the compound middle lamella intact (Figs. 4i and 5i).

3.2. Static and dynamic mechanical properties

As illustrated in Fig. 6, the impact of the two fungal species on *MOR*

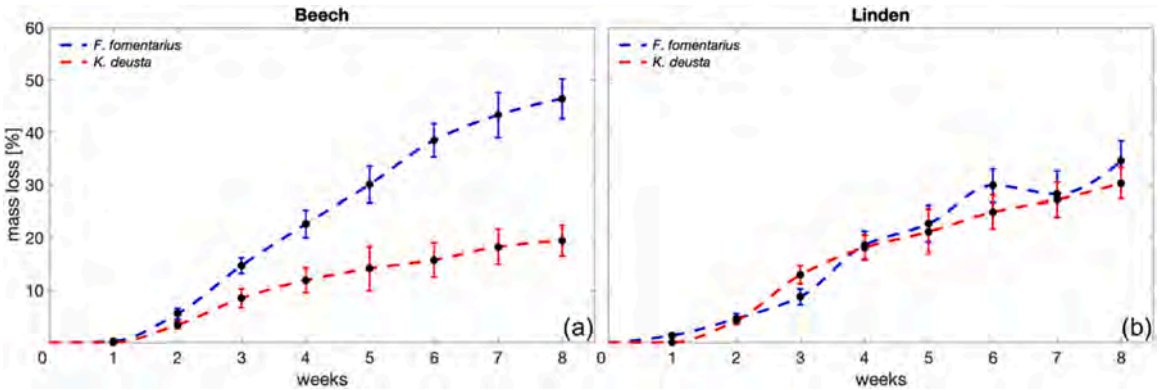

Fig. 3. *ML* mean values for beech (a) and linden (b) specimens with their standard deviation after all exposure periods.

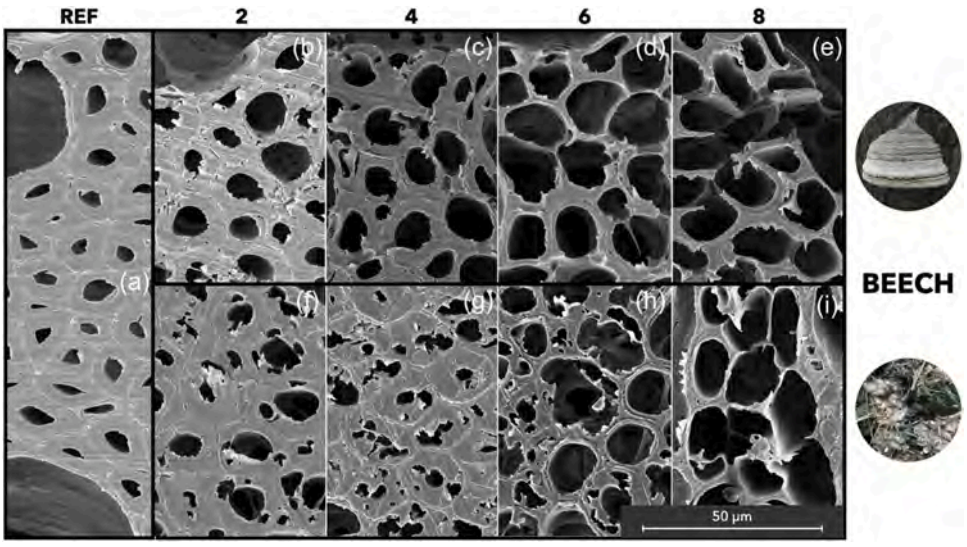

Fig. 4. SEM scans of beech samples after 2, 4, 6 and 8 weeks of exposure to *F. fomentarius* (b-e) *and K. deusta* (f-i) enzymatic activity in comparison to an intact sample (a).

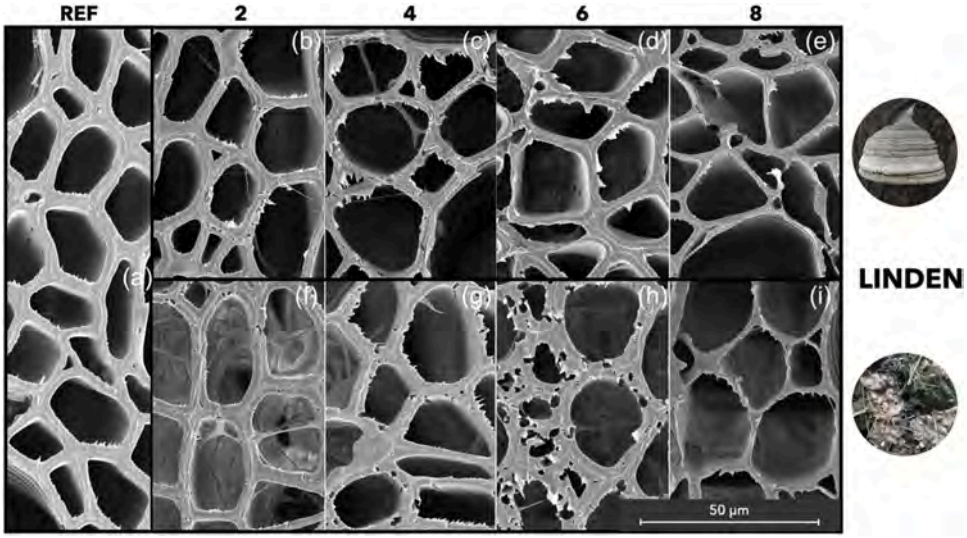

Fig. 5. SEM scans of linden samples after 2, 4, 6 and 8 weeks of exposure to *F. fomentarius* (b-e) *and K. deusta* (f-i) enzymatic activity in comparison to an intact sample (a).

and *MOED* varied according to the species of the colonized wood. According to the data presented in Table 1, in beech wood, *F. fomentarius* led to advanced degradation, resulting in a mean *MOR* of 9.24 MPa after 8 weeks of exposure, which corresponds to 15.18 % of the mean *MOR* for intact reference specimens. In contrast, degradation by *K. deusta* was less severe, leading to a final *MOR* of 27.11 MPa (44.55 % of the *MOR* measured for intact samples). The difference in *MOR* for beech wood between the two fungal species increased gradually (Fig. 6a).

According to a non-parametric ANOVA, there was no statistically significant difference between the two fungal species during the first two weeks of exposure ($p > 0.001$). However, a significant difference in mean values was established for the later exposure periods (from the third to the eighth week). *MOED* values for beech wood exhibit a similar trend (Fig. 6c); however, significant differences between the two species become apparent at more advanced stages. No statistically significant difference between *F. fomentarius* and *K. deusta* in beech wood was identified for the first five weeks ($p > 0.001$). Yet, from the sixth week of exposure onwards, the values were shown to be statistically different. In the final stage of exposure to *F. fomentarius*, the mean *MOED* for beech wood was recorded at 2.29 GPa (Table 1), representing 20.74 % of the intact *MOED*, while *K. deusta* resulted in a final mean *MOED* of 5.04 GPa, equating to 45.65 % of the reference value.

For linden wood, both fungal species exhibited a similar influence on its static and dynamic mechanical properties (Fig. 6b,d). Regarding the *MOR* values of degraded linden, no statistically significant differences between *F. fomentarius* and *K. deusta* were identified for any period of exposure. As indicated in Table 2, in the final stage of degradation, *F. fomentarius* resulted in a mean *MOR* of 8.95 MPa, while *K. deusta* led to a *MOR* of 6.68 MPa (32.62 % and 24.34 % of the intact reference value). The distribution of *MOED* values for linden wood mirrors that of *MOR* (Fig. 6d), with the only statistically significant difference between the two fungi observed during the fourth week of exposure ($p < 0.001$). *F. fomentarius* resulted in a *MOED* equal to 39.93 % of intact specimens' *MOED*, whereas *K. deusta* had a more pronounced effect, reducing *MOED* to 26.91 % of the reference value (Table 6). The variability (CV) in *MOR* across different exposure periods ranged from 8.57 % to 46.57 %. Similarly, for *MOED*, the variability ranged from 6.51 % to 46.27 %.

As shown in Fig. 7a and b, a strong relationship between *ML* and

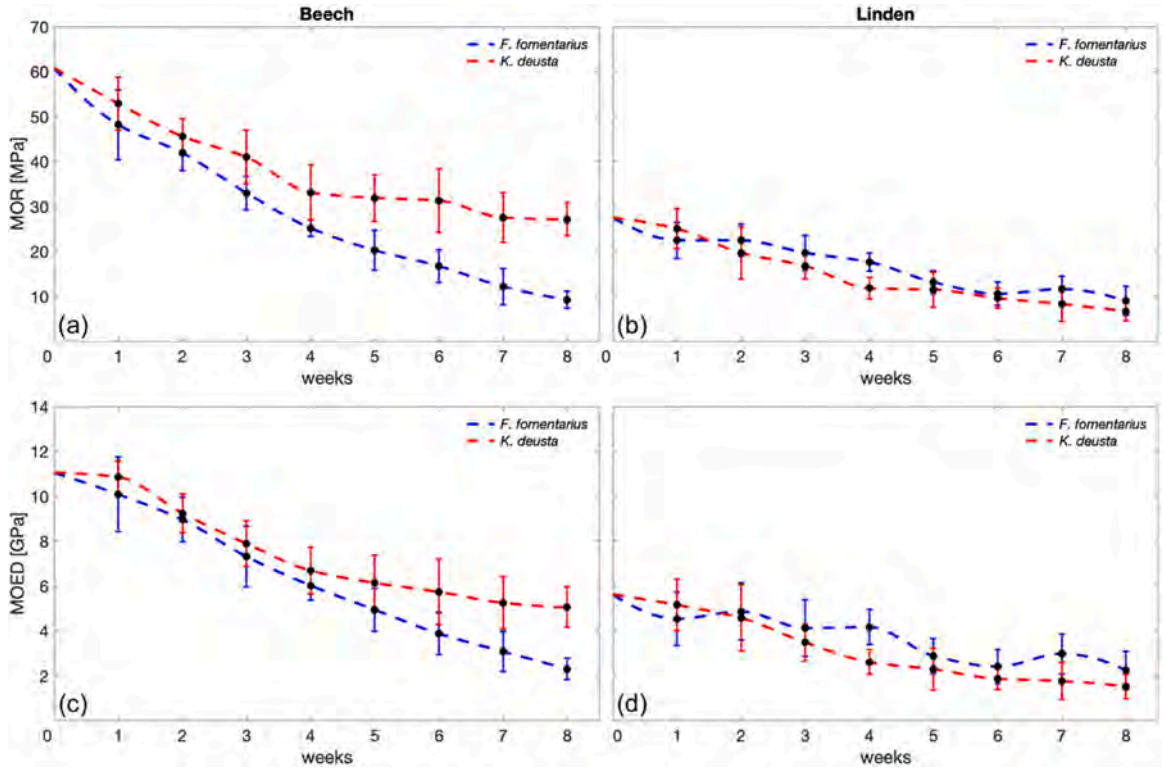

Fig. 6. mean *MOR* (a,b) and *MOED* (c,d) values for beech and linden specimens with their standard deviation after all exposure periods and intact reference specimens.

Table 1
Mean values of physical and mechanical properties of degraded beech bending samples after each exposure period (week) and intact reference samples (ref).

	Beech									
	F. fomentarius					*K. deusta*				
Week	***MOR*** (MPa)	MOED (GPa)	***MC*** (%)	ρ_w (kg/m^3)	***ML*** (%)	***MOR*** (MPa)	MOED (GPa)	***MC*** (%)	ρ_w (kg/m^3)	***ML*** (%)
1	48.17	10.08	68.8	948.32	0.26	52.89	10.85	80.93	1023.67	0.02
2	41.9	8.95	65.81	868.02	5.49	45.6	9.23	98.63	1078.82	3.37
3	32.98	7.31	81.36	878.61	14.68	40.95	7.88	91.57	977.20	8.45
4	25.17	6.02	75.71	763.73	22.6	33.09	6.68	88.4	925.29	11.87
5	20.25	4.94	99.48	778.64	30.09	31.88	6.13	86.92	896.47	14.11
6	16.72	3.87	119.81	770.84	38.47	31.29	5.73	88.30	892.15	15.75
7	12.17	3.01	107.40	665.5	43.29	27.5	5.25	93.86	884.5	18.26
8	9.24	2.29	139.8	729.53	46.40	27.11	5.04	104.16	912.53	19.43
ref	60.85	11.04	65.38	922.46						

Table 2
Mean values of physical and mechanical properties of degraded linden bending samples after each exposure period (week) and intact reference samples (ref).

	Linden									
	F. fomentarius					*K. deusta*				
Week	***MOR*** (MPa)	MOED (GPa)	***MC*** (%)	ρ_w (kg/m^3)	***ML*** (%)	***MOR*** (MPa)	MOED (GPa)	***MC*** (%)	ρ_w (kg/m^3)	***ML*** (%)
1	22.49	4.53	102.13	722.93	1.36	25	5.15	135.26	843.52	0.05
2	22.48	4.86	117.52	768.92	4.56	19.64	4.57	159.92	902.41	4.18
3	19.66	4.11	151.01	830.72	8.74	16.74	3.48	170.71	870.18	12.8
4	17.61	4.16	120.8	672.53	18.58	11.79	2.6	206.82	909.83	18.12
5	13.14	2.88	138.36	680.28	22.66	11.48	2.28	198.67	841.2	21.13
6	10.55	2.4	161.99	682.19	29.89	9.58	1.86	197.06	795.29	24.86
7	11.61	2.97	182.13	740.45	28.26	8.26	1.76	210.04	827.05	27.18
8	8.95	2.24	261.68	844.56	34.51	6.68	1.51	224.67	820.94	30.3
ref	27.44	5.61	98.94	731.52						

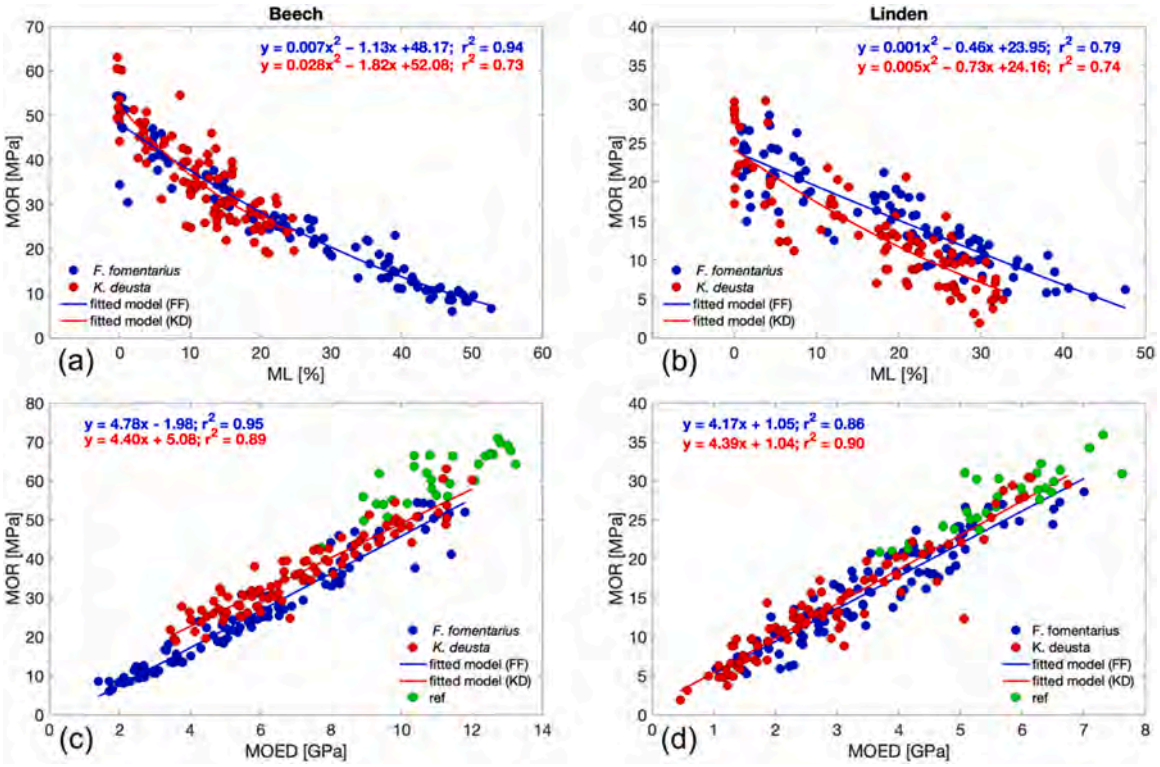

Fig. 7. relationships between *ML* –*MOR* and *MOED* –*MOR* for beech (a,c) and linden (b,d) exposed to *F. fomentarius* (blue) and *K. deusta*. The *MOED* –*MOR* plots include values from intact reference samples (ref).

MOR was established for all fungus-wood combinations. The most pronounced quadratic relationship was observed for beech wood and *F. fomentarius* ($r^2 = 0.94$), while the least strong was for beech wood and *K. deusta* ($r^2 = 0.73$). The weaker rate of *MOR* reduction at more advanced stages of decay indicates that a linear trend does not adequately describe the relationship between *ML* and *MOR*. This pattern was previously identified by Curling et al. (2002), who noted that the relationship between *ML* and *MOR* in southern pine caused by two brown-rot fungi was linear up to 20 % *ML*, beyond which the rate of *MOR* reduction decreased.

The *ML* –*MOR* relationships for the two fungal species exhibit slight variations, particularly in linden wood (Fig. 7b), where at equivalent *ML* values, *K. deusta* resulted in a more significant reduction in MOR.

According to Fig. 7c-d, a strong linear relationship between *MOED* and *MOR* was established for all fungus-wood combinations. In every instance, the *MOED* –*MOR* relationship proved to be stronger, even if slightly, than the *ML* –*MOR* relationship. The most significant difference was observed in both wood species exposed to *K. deusta*, with *ML* –*MOR* r^2 values of 0.89 for beech and 0.90 for linden, respectively. Unlike the *ML* –*MOR* relationships depicted in Fig. 7a and b, the correlation between *MOED* and *MOR* appears very similar for both fungal species across the wood types.

4. Discussion

4.1. Comparison of ML and decay patterns between wood and fungal species

Comparing the overall degradation rates caused on both wood species, similar average *ML* values were observed by the end of the experiment. Although there is a statistically significant difference in the *ML* rate at the late stages for each fungus between the two wood species ($p < 0.001$), *F. fomentarius* caused higher *ML* in beech wood, while *K. deusta* led to higher *ML* in linden. These findings indicate that the significant difference in ρ between the two species (Kretschmann, 2010) does not significantly affect the intensity of wood degradation. These results are consistent with the conclusions drawn by Plaschkies et al. (2014), who explored the natural durability of different species and found only a weak correlation between ρ and degradation rate for larch, but not for other species.

The higher degradation rate observed in linden samples due to *K. deusta* aligns with findings presented by Schwarze et al. (1995), who examined the degradation patterns of *K. deusta* on beech and large-leaved linden wooden blocks. After 12 weeks of fungal exposure, beech blocks exhibited a mean ML of 4.6 %, while linden blocks showed 8.3 %. The same beech wooden blocks were also exposed to *F. fomentarius*, resulting in a final mean *ML* of 21.2 %, demonstrating a similar wood/fungus interaction as described in this study. Schwarze et al., (2004) also highlighted the susceptibility of linden wood to degradation caused by *K. deusta*, in comparison to beech wood. However, the distinction between the two wood species presented in this article is not as pronounced, partly because the primary difference described by the authors pertains to wood in standing trees, where parenchyma cells perform an irreplaceable role in limiting fungal degradation. Deflorio et al. (2008) demonstrated that degradation caused by *K. deusta* on artificially inoculated standing beech trees resulted in ML of 13.4 % over 27 months. This comparatively low *ML* value, relative to the results presented in this study, can be attributed to the different degradation dynamics between standing trees and wooden specimens in the laboratory, where environmental conditions are not directly comparable. The significant differences in *ML* values observed in beech wood due to the two fungal species (Table 1) are consistent with the findings of Cristini et al. (2023, 2022). In these studies, after a 12-week exposure period, *F. fomentarius* resulted in an average *ML* of 65.8 %, compared to 31 % caused by *K. deusta*. Based on these findings, we can suggest that *K. deusta* leads to more severe degradation in linden compared to beech, while *F. fomentarius* showed greater degradation in beech wood. This is partially supported by its common occurrence in

beech trees with a high risk of structural failure (Schwarze et al., 2004). However, it's important to note that this study focuses mainly on wood as a material. In living trees, degradation can be influenced by other factors, such as the interaction and competition between different fungal species, the activity of living tissues within the wood and reaction growth, which should be considered.

According to Figs. 4 and 5, *F. fomentarius* did not produce cavities in the S2 layer similar to type I soft-rot decay, as has been previously documented (Cristini et al., 2023). It has been shown that various WRF can cause soft-rot decay patterns (Bari et al., 2020; Schwarze et al., 1995b), but this seems to only occur under specific environmental conditions. The preservation of the compound-middle lamella after exposure to *K. deusta* is likely due to the high content of Guaiacyl lignin, which is typical for hardwood species (Schwarze et al., 1995). Based on the SEM scans presented, it is evident that the decay patterns caused by the individual fungal species did not vary according to the wood species.

4.2. Influence of external factors

The differences in decay behaviour between *F. fomentarius* and *K. deusta* across the two wood species may be affected by various factors, such as moisture content (*MC*) and access to oxygen (Kazemi et al., 2001). As indicated in Tables 1 and 2, the *MC* range for beech and linden wood significantly differs (65.81 % −139.8 % for beech, 102.13 % −261.68 % for linden). However, the original absolute water content of the specimens prior to sterilization was comparable (ranging from 1.8 to 2.2 g). Consequently, the notable difference in *MC* is attributed to the distinct porosity levels of the two wood species. From this inference, it is suggested that the volume of air within the samples was relatively similar, thereby discounting the original *MC* as a factor affecting the degradation rate. Within each wood species, no statistically significant difference in *MC* was observed across the various exposure periods ($p > 0.001$). As illustrated in Tables 1 and 2, *Sc* tends to rise alongside higher ML values. Significant correlations between *ML* and *MC* were established for beech samples exposed to *F. fomentarius* ($Sc = 0.62$) and for linden exposed to both *F. fomentarius* ($Sc = 0.67$) and *K. deusta* ($Sc = 0.57$). However, for the combination of beech and *K. deusta*, no significant correlation between *MC* and *ML* was identified ($Sc = 0.22$). Zelinka et al. (2020) also demonstrated a significant correlation between *MC* and *ML* in southern pine wood exposed to the fungus *Rhodonia placenta* (Fr.) Niemelä, K.H. Larss. & Schigel. Similarly, Bari et al., (2020) identified the same relationship in beech wood for the fungal species *Pleurotus ostreatus* (Jacq.) P. Kumm. and *Trametes versicolor* (L.) Lloyd. This correlation is attributed to the progressive production of water during the metabolic activity of the fungus (Zabel and Morrell, 2020). Therefore, given that the initial water content was comparable for both wood species and that temperature and air humidity were kept constant throughout the exposure period, it can be concluded that the differing dynamics of degradation are primarily determined by the wood species involved. Considering the original water content of both wood species at the beginning of fungal exposure to be comparable, and that the correlation between ML and MC is caused by the progressive enzymatic activity of the fungi, we can state that the difference in decay dynamics in the two investigated wood species was not influenced by MC. Therefore, these differences could have been caused by other factors, such as submicroscopic cell structure or chemical composition.

4.3. Static and dynamic mechanical properties

Cristini et al. (2023) assessed the mechanical properties of beech wood following laboratory exposure to *F. fomentarius*, reporting even lower *MOR* and *MOED* values after 8 weeks of exposure (6.3 MPa; 1.68 GPa). However, given the inherent variability of wood, which is further enhanced by fungal degradation, these differences in measured mechanical properties are not considered significant. Schwarze et al. (1995) observed an 85 % reduction in the strength of beech increment cores exposed to *F. fomentarius* for 4 weeks. The rapid decline in ultimate stress, compared to our study's findings (*MOR* loss after 4 weeks of inoculation compared to intact samples = 58.64 %), can be attributed to the sample orientation, allowing the fungus to spread parallel to the grain from the surface directly through the entire cross-section of the samples laid on the mycelium. Cristini et al. (2022) investigated the static and mechanical properties of beech wood after 12 weeks of exposure to *K. deusta*. The *MOR* and *MOED* values after this period (25.5 MPa; 4.25 GPa) showed low deviation from those observed after 8 weeks of exposure in this study (Table 1), leading to the conclusion that the most significant impact on the mechanical properties of beech occurs during the initial exposure phase.

Slight variations of the *ML* −*MOR* relationships each wood species may be caused by the different decay types exhibited by the investigated fungi, which could impact the mechanical properties of the libriform fibres differently. Another contributing factor could be the heterogeneity of fungal degradation. Comparative exposure of small bending beech wood samples to *F. fomentarius* (Cristini et al., 2023) and *K. deusta* (Cristini et al., 2022) revealed greater heterogeneity in degradation across the length of the samples with *K. deusta*. This variability can adversely affect standard static mechanical testing, which assumes material homogeneity (de Almeida et al., 2018).

The similarity of the *MOED* – *MOR* relationships for both fungal species across the wood types proves that vibro-acoustic parameters not only provide a more accurate description of static mechanical properties at the dynamics of degradation (as evidenced by the proximity of the measured data to the computed linear model) but also offer consistency across different types of decay (in this case white and soft rot). Furthermore, the computed model can be applied to the assessment of both degraded and intact samples, simplifying the analysis and interpretation of results obtained from non-destructive vibro-acoustic testing. This strong relationship was already confirmed for both fungal species on beech wood (Cristini et al., 2023, 2022); however, these studies primarily examined advanced decay stages (8 and 12 weeks of exposure) and focused solely on one wood species. The linear model for beech samples exposed to *F. fomentarius*, as presented by Cristini et al. (2023) was not applicable to intact samples, probably due to the already significant advancement in decay (*ML* range from 43 % to nearly 80 %). It appears that the same linear model can accurately predict the strength of both degraded and intact samples, but only in cases of early decay stages. Nevertheless, during the non-destructive evaluation of tree stability, the initial stage of decay is the most crucial, as significant strength loss occurs in the early phase of degradation (Curling et al., 2002).

5. Conclusion

Considering the previously presented and discussed results, the following conclusions can be drawn:

- Except for the first week of exposure, the *ML* in beech wood caused by *F. fomentarius* was higher and statistically distinct from the *ML* caused by *K. deusta*. In linden, after excluding the first period of exposure, no significant difference in *ML* between the two fungal species was established. *F. fomentarius* led to higher *ML* in beech, whereas *K. deusta* had a more pronounced effect on linden.
- SEM assessments at various stages of decay revealed that *F. fomentarius* exhibited patterns typical of simultaneous white-rot decay, whereas *K. deusta* caused a type I soft rot. Morphological changes were consistent across both wood species (Figs. 4, 5).
- In beech wood, the difference in *MOR* and *MOED* between the two fungal species became more pronounced as degradation progressed (Fig. 6): a significant difference in *MOR* between the two fungal species was observed starting from the third week of exposure, and for *MOED* from the sixth week. For *MOR* and *MOED* values of degraded linden, except for the fourth week of exposure, no significant differences between the two fungi were detected.

- Across both wood species, the relationship between *ML* and *MOR* varied depending on the fungus, with *ML* caused by *K. deusta* resulting in greater *MOR* loss (Fig. 7). This difference may be attributed to the type of decay or, more likely, to the greater heterogeneity in density distribution caused by *K. deusta*'s degradation. In all instances, a significant quadratic relationship was established for all wood-fungus combinations (r^2 from 0.73 to 0.94).
- The *MOED* −*MOR* relationship (Fig. 7) was consistently stronger than the *ML* −*MOR* relationship (r^2 from 0.86 to 0.95). The models fitted for both fungal species were very similar, irrespective of the type of decay. The linear models demonstrated greater precision in predicting MOR at early stages of decay and can be applied to estimate static properties of both degraded and intact wood.

The findings of this study have demonstrated distinct decay patterns of *F. fomentarius* and *K. deusta*, varying according to the colonised wood species (beech and linden). Both fungal species are associated with the structural collapse of standing trees, and the provided results can enhance our understanding and prediction of their impact on the host species under investigation. Additionally, the presented relationship between dynamic and static mechanical parameters can be applied to improve the results of non-destructive, device-supported methods for assessing tree stability.

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CRediT authorship contribution statement

Jan Tippner: Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Jan Zlámal:** Writing – review & editing, Investigation, Data curation. **Patrik Nop:** Writing – review & editing, Investigation, Data curation. **Valentino Cristini:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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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