RESEARCH ARTICLE

Warming effects on wood decomposition depend on fungal assembly history

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Abstract

1. Climate warming has the potential to drive changes in fungal community development and dead wood decomposition, but our understanding of this process is obscured by complex interactions between temperature and multiple other factors. A pivotal factor driving decay dynamics is fungal assembly history, yet its response to elevated temperature is poorly understood.

2. We investigated the combined effect of warming and assembly history on community composition, respiration and decomposition using experimental communities of wood-decaying fungi on spruce wood. Assembly histories were assigned to microcosms under normal and elevated temperatures in a factorial design.

3. Both temperature and assembly history influenced wood mass loss and respiration. Temperature was the most important factor, but the effects of warming on decomposition varied greatly with fungal assembly history. Depending on which fungal species colonized first, warming of 5°C increased wood mass loss by 7%–57% after 9 months. The large variation in decomposition response to warming resulted from differential responses in the growth of initial colonizers (pre-inoculated) and their competitive ability, resulting in different decomposer communities.

4. *Synthesis*. Our study demonstrates that temperature and assembly history jointly determine deadwood decomposition and fungal community composition under controlled laboratory conditions. Further investigations are needed to confirm these results under natural conditions. Nevertheless, our findings highlight the importance of considering interactions between priority effects and climate factors to understand forest carbon feedbacks in the context of climate change.

KEYWORDS

CO_2 feedback, community composition, ecosystem function, global warming, interactions, priority effects, saprotrophic fungi, temperature

1 | INTRODUCTION

Many ecosystem processes, including decomposition of organic matter, are expected to be considerably influenced by climate warming (Crowther et al., 2016; Lu et al., 2013). The effect of warming on terrestrial carbon storage is, however, very complex. Although it is well established that the direct effect of moderate warming is a general increase in decomposition rates (Conant et al., 2011),

the importance of indirect effects remains poorly understood (Bardgett et al., 2008; Rubenstein et al., 2017). Indirect effects of warming have the potential to amplify or dampen the direct effect and a better understanding of their influence on decay dynamics is therefore needed (A'Bear, Crowther, et al., 2013; Glassman et al., 2018; Romero-Olivares et al., 2017). One of the greatest uncertainties concerns how climate change affects the decomposer community structure and how this, in turn, influences decomposition rates (Bardgett et al., 2008; Karhu et al., 2014). A prime cause of this uncertainty is that multiple drivers of microbial community change are likely to work in concert, with complex interactions and feedbacks (Crowther et al., 2012; Venugopal et al., 2017).

Saprotrophic fungi are the primary decomposers of dead wood and litter in boreal and temperate forests and play a crucial role in the regulation of terrestrial carbon dynamics (Boddy et al., 2008). The composition of fungal communities in woody tissue is largely determined by the outcome of competitive interactions, which are influenced by biotic (e.g. resource quality and grazing) and abiotic factors (e.g. temperature and moisture; Boddy, 2000). Temperature is an important regulator of fungal growth and enzyme activity, and thus a crucial driver of decay dynamics (Conant et al., 2011). Optimal temperature differs between species and even moderate warming can alter outcomes of fungal interactions in wood and soil (Crowther et al., 2012; Hiscox, Clarkson, et al., 2016; Venugopal et al., 2016). Since different species use functionally different mechanisms to degrade wood (e.g. white and brown rot), a shift in the fungal community structure has the potential to cause a significant change in decomposition rate (van der Wal et al., 2015).

It is well established that development of fungal communities in wood is profoundly influenced by assembly history, that is, the order and timing of species establishment in a community (Dickie et al., 2012; Fukami et al., 2010; Hiscox, Savoury, Muller, et al., 2015; Leopold et al., 2017; Niemela et al., 1995; Ottosson et al., 2014). Depending on which species initiate decomposition, secondary colonizers may be inhibited, facilitated or unaffected (Niemela et al., 1995; Tiunov & Scheu, 2005). The initial species may affect secondary species directly via mycelial interactions and/or indirectly through chemical and physical modification of the substrate (Allison, 2012; Hiscox, Savoury, et al., 2016; Holmer et al., 1997). These effects, known as priority effects, can be influenced by abiotic and biotic factors and are important drivers of fungal community development and decomposition (Cline & Zak, 2015; Hiscox, Savoury, et al., 2016; Leopold et al., 2017). However, priority effects are rarely considered in decomposition studies, which may contribute to explaining the idiosyncrasies often observed in carbon dynamics (Fukami et al., 2010; Hiscox, Savoury, Muller, et al., 2015). In addition, although the importance of priority effects in wood decay dynamics is well recognized, we still have limited understanding of how the strength of these effects may change when environmental conditions are altered, such as under climate warming.

New wood resources (without endophytes) are colonized by early successional fungi, usually by spores from which mycelia develop (Boddy & Hiscox, 2016). Some species are also able to enter via mycelial cords or rhizomorphs, and in angiosperms colonization may be initiated from latent fungal propagules within functional sapwood (Parfitt et al., 2010). The colonization history of species arriving as spores is rather stochastic and depends on multiple factors such as sporulation timing, phenology of insect vectors, enzymatic capacity of the fungus, micro environmental factors and spore traits, in combination with prevailing weather conditions (Boddy & Hiscox, 2016; Jacobsen et al., 2018; Norros et al., 2014). Once established, the mycelia strive to expand and defend their territory. It is well recognized that the strength of priority effects may depend on the physiological traits of early colonizers. For example, organisms with a fast growth rate may gain a competitive advantage when arriving early in a habitat (Cline & Zak, 2015; Vannette & Fukami, 2014; Vaughn & Young, 2015). Hence, in addition to enzymatic capacity, stress tolerance and competitive traits, a species' initial growth rate after colonization could potentially be an important contributing factor determining its establishment success and future impact on the fungal community development in wood.

Given that temperature is an important regulator of fungal growth and competitive ability, and that species have different optima for this factor, climate warming has the potential to greatly influence the relative impact of different early fungal colonizers in wood (Crowther et al., 2012; Hiscox, Clarkson, et al., 2016). If so, fungal community composition is likely to be modified, with consequences for fungus-mediated decomposition rates. In this study, we performed a laboratory microcosm experiment with wood-decaying fungi to test for combined effects of assembly history and warming on fungal growth, community development and decomposition. The microcosm approach allows for rigorous experimental control that is often necessary to provide a mechanistic understanding of complex processes such as decomposition and fungal interactions in wood. We predict that both temperature and assembly history are important in determining fungal community composition and wood decay rates. However, we also expect interactions between these factors. As early fungal colonizers have the potential to respond differently to an elevated temperature, we hypothesize that their relative influence on the community development will be modified by warming, with consequences for respiration and wood decomposition rates. Here we tested these hypotheses by pre-colonizing wood-discs with one of eight species before introducing the other seven species. Wood-discs were incubated at normal and elevated temperatures for 9 months, followed by analyses of wood mass loss and characterization of species composition and richness. Initial growth of pre-inoculated fungi was assessed and respiration monitored over time.

2 | MATERIALS AND METHODS

2.1 | Experimental fungi

Multiple strains of 30 species of wood-decay basidiomycetes were isolated from fruiting bodies collected from fairly fresh (c. 2–10 years old) Norway spruce and Scots pine logs in spruce-dominated forests close to Sundsvall, central Sweden. Pure cultures were obtained using a 2% malt extract medium supplemented with thiabendazole

TABLE 1 No. of strains, type of rot, host tree preference (D = deciduous, P = pine, S = spruce) and preferred decay stages of the included species. The preferred decay stage is based on incidence of fruiting bodies on natural logs (Renvall, 1995). Decay stages 1–5 indicate the average decay stage of the wood; where stage 1 represent fresh wood and stage 5 very decayed wood

Scientific name	Acronym	No. of strains	Rot type	Host trees	Average decay	Decay range
Antrodia sinuosa (Fr.) P. Karst.	As	8	Brown	P, S	2.8	1–4
Antrodia xantha (Fr.) Ryvarden	Ax	5	Brown	P, S, D	2.6	1–5
Climacocystis borealis (Fr.) Koutl. & Pouzar	Cb	7	White	S	2.4	1–3
Fomitopsis pinicola (Sw.) P. Karst.	Fp	8	Brown	S, P, D	2.6	1–4
Fomitopsis rosea (Alb. & Schwein.) P. Karst.	Fr	8	Brown	S	2.8	2–5
Gloeophyllum sepiarium (Wulfen) P. Karst.	Gs	8	Brown	S, P	2.4	1–4
Phlebia centrifuga P. Karst.	Pc	6	White	S	2.4	1–4
Phellinus ferrugineofuscus (P. Karst) Bourdot	Pf	8	White	S	2.7	1–4

(230 mg/L) and the selective fungicide benomyl (2 g/L). Eight species were selected for experimental use based on the feasibility of handling them, whether they can be identified in culture and depending on the number of available strains. Species identity of each strain was confirmed by comparing its morphology (colour, texture etc.) in culture with sequenced reference cultures belonging to the Mid Sweden University Fungi Collection (Table S1). To ensure proper replication and cover intraspecific variation, we isolated eight strains per species, except for three species for which only 5, 6 and 7 strains were available respectively (Table 1). The selected species represent various habitat preferences and functional traits, such as different rot types (white and brown rot) and tree species preferences (Table 1). They are all characteristic species for Scandinavian boreal forests and are widely distributed in boreal conifer regions of the world. All species are able to colonize and decay fresh spruce wood, which was confirmed by growing them on fresh wood discs before conducting the experiment. In addition, since hetero- and monokaryotic strains of a species may behave differently (Crockatt et al., 2008), we confirmed that strains were heterokaryotic by checking for the presence of clamps, a mycelial structure on heterokaryons, using a microscope. However, *Phellinus ferrugineofuscus* could not be confirmed as heterokaryotic by this method because it does not form clamps on its heterokaryons. Fungal cultures were maintained on malt agar plates (MA) prior to experimental use.

2.2 | Wood material and preparation of microcosms

Three healthy 12-year-old Norway spruce trees (*Picea abies* L. Karst.) with a base diameter of 9 cm were collected from a plantation and cut into 1-cm thick, 8-cm-diameter discs. The wood discs were oven dried at 40°C to constant weight, and thereafter individually weighed (initial dry weight 18.4 ± 1.9 *SD*). They were then soaked in water over night and sterilized by autoclaving three times at 121°C

for 15 min. Working in a laminar flow cabinet the wood discs were placed in sterile 500-ml glass jars (IKEA, Sweden) containing 110 ml of perlite wetted with 65 ml water to maintain a stable humidity in the jars. Wood discs were randomly assigned to jars. The jars were closed with their lids but after inoculation of the first fungal species, lids were removed and the jars were instead covered by a 10-cm wide, stretched parafilm to allow gas exchange but retain moisture. The jars were regularly checked for contamination throughout the experiment.

2.3 | Manipulation of assembly history

Assembly history was manipulated by inoculating one species 2 weeks ahead of the rest. From 2-week-old cultures on MA plates, 5-mm thick plugs of each species were punched with an 8-mm diameter sterilized cork borer and inoculated onto pre-determined locations on the wood discs (cf Fukami et al., 2010; Figure 1). The species' fixed, pre-determined locations were chosen randomly. All species were used as the pre-inoculant, while keeping species' relative position constant between replicates. Different strains of both pre-inoculated and later inoculated species were used in all eight replicates for each assembly history (Figure S1), except for the three species for which only 5, 6 and 7 strains were available (Table 1).

2.4 | Temperature treatment

To emulate the current and predicted elevated temperatures, microcosms were placed in two Termaks 6000 cooling incubators (Termaks AS, Norway). The experiment had a completely randomized factorial design (Figure S1). It was run for 9 months, and temperatures were changed once a month to emulate average monthly temperatures
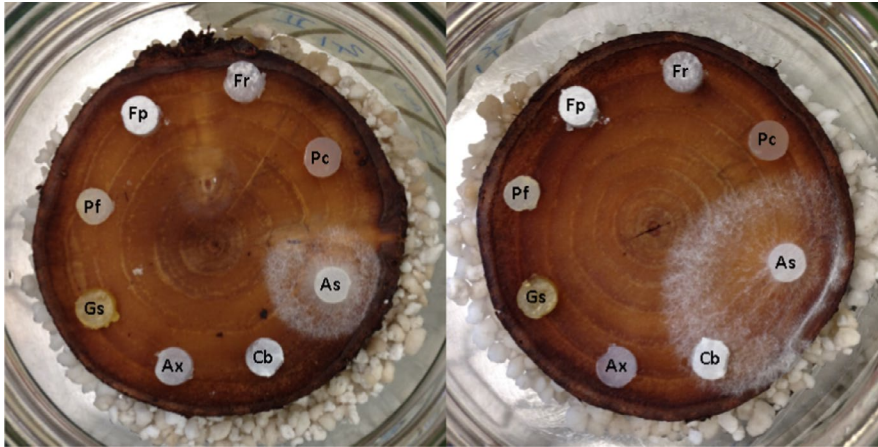
FIGURE 1 An example of the experimental set up, showing 2 weeks growth of the pre-inoculated species *Antrodia sinuosa* (As) under normal (12°C, left image) and elevated (17°C, right image) August temperature on 8-cm diameter wood discs, contained in glass jars with wetted perlite. When the photograph was taken the rest of the species had recently been added (species acronyms as in Table 1)

for the middle boreal zone of Sweden, although relevant for a large part of the boreal zone. Normal temperatures were based on average monthly temperatures during the period 1961–1990 according to the Swedish Meteorological and Hydrological Institute (SMHI). Elevated monthly temperatures were based on the regional climate projections of the Rossby Centre (SMHI) until 2,100 in the same region (Table S2). We used regional projections based on scenario RCP8.5 (IPCC, 2013), which projects an average future warming of about 6°C in the boreal region by 2,100. RCP8.5 is a scenario of comparatively high greenhouse gas emissions, but is closest to the emission trends currently being recorded. For technical reasons, only months with a normal average temperature of >0°C were included, while November, December, January, February and March were excluded. August temperatures were used at the start of the experiment as many wood-decaying fungi start to produce fruiting bodies, release spores and colonize new substrates at this time of the year in boreal forests (Halme & Kotiaho, 2012). The treatment continued with September to July temperatures, and thereafter August and September temperatures were repeated before ending the experiment. In total, nine temperature cycles were run, each lasting *c.* 30 days, with an average temperature of 8.6 and 14°C in normal and elevated temperature regimes respectively. The difference in temperature between treatments was on average 5.4°C.

2.5 | Measurement of initial mycelial growth

To determine the response of pre-inoculated fungi to increased temperature, we recorded their mycelial growth rate (mm/day) during the first 2 weeks, before the rest of the species were added. Mycelial growth was measured as the radial extension from the edge of the agar plug towards the centre of the wood disc. The temperature treatment was represented by August's normal (12°C) and elevated (17°C) temperatures.

2.6 | CO_2 measurements

CO_2 production was measured after 4, 5, 6 and 9 months, representing April, May, June and September temperatures respectively. At each of the designated time points the Parafilm was removed from jars and microcosms were ventilated in a sterile laminar flow cabinet for 5 min at the same temperature as the current treatment temperature. They were then closed with new Parafilm as well as with an airtight lid and incubated in the climate cabinets for a fixed period of time to accumulate CO_2. Since CO_2 production increased over time as decomposition progressed, we needed to adjust the time for accumulation between sampling occasions to avoid CO_2 saturation. To find appropriate incubation times, CO_2 accumulation was tested on a subset of microcosms not included in the experiment. The incubation time when jars were closed to accumulate CO_2 after ventilation was 12 hr, 6 hr and 40 min for the first, second and last two measurements respectively. After incubation, the lid was removed from each jar and a 10-ml air sample was drawn through the parafilm using a syringe; it was then injected into an EGM-4 Environmental Gas Monitor (PP systems, USA).

2.7 | Wood mass loss calculation and preparation for species detection

The dry weight of the wood discs was measured at the end of the experiment after drying to constant weigh at 40°C. Prior to drying, sawdust samples were taken from the discs for re-isolation and molecular analysis of fungal species composition. Using a sharp knife and a rubber maul, discs were split along eight radial lines into eight equally sized pieces, where each piece represented the inoculation point of a pre-inoculated species (Figure S2; cf Fukami et al., 2010). Each piece was drilled to produce sawdust at three standard locations using ethanol-flamed 4-mm drill bits (Figure S2). The pooled wet weight of the three sawdust samples from each wood piece was recorded before being placed in ziplock bags and frozen at −20°C whilst awaiting DNA extraction. To calculate the total dry weight of the discs, we first calculated the dry weight of the removed sawdust by dividing the product of *dry weight of drilled disc × wet weight of sawdust* with the wet weight of the drilled disc. The dry weight of the sawdust was, on average, 1.1 (±0.2 *SD*) g, representing 7.6% of the total dry weight. The total percentage wood mass loss (including fungal biomass) could thereafter be calculated as the difference between initial and final dry weight divided by initial dry weight.

2.8 | Species abundance

The abundance of each species per disc was determined by re-isolation from the sawdust samples. From each drill sample, 0.5 ml sawdust was inoculated onto 2% MA and incubated at 20°C until mycelia had emerged and could be identified morphologically (cf. Edman & Eriksson, 2016). Abundance was scored as the number of wood pieces (Figure S2) that a species was present in. To confirm the accuracy of the method we also performed a molecular analysis of 40 randomly selected sawdust samples (Appendix S1). PCR confirmed the results of the re-isolation method, although the match was not perfect. The re-isolation method found 91% ($\pm$3.4 *SE*) of the records detected by PCR and PCR found 73% ($\pm$6.1 *SE*) of the records detected by re-isolation. The difference in detection was probably mainly a result of more material being used for re-isolation.

2.9 | Data analysis

The effect of assembly history and warming on fungal community composition was tested with a multivariate generalized linear model with negative binomial error distribution, using the function ManyGLM in the R-package MVABUND (Wang et al., 2012). Model assumptions were evaluated by examining residual plots (Wang et al., 2012). To visualize differences in fungal communities between treatments we used nonmetric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities. In addition, to test the effect of experimental treatments on individual species abundance at the end of the experiment we used GLM with the proportion of colonized subsamples per microcosm as a binomial response and a logit link function. Models were simplified using a stepwise backward selection based on likelihood-ratio tests. A similar GLM was also used to test the importance of temperature and species identity for the long-term prevalence of pre-inoculated fungi. In this case, the binomial response was the proportion of subsamples (per microcosm) colonized by the pre-inoculated species. We also ran a binomial GLM to test for effects of temperature and initial species on the number of species remaining at the end of the experiment. Post hoc comparisons (Tukey's HSD) were performed with the R package EMMEANS (Lenth, 2019). The relative importance of predictors in the GLMs was calculated with the R package DOMINANCEANALYSIS using McFadden's pseudo-R^2 (Bustos Navarette & Coutinho Soares, 2020).

The effect of temperature and pre-inoculated species (assembly history) on wood mass loss and initial mycelial extension rate was analysed with two-way ANOVAs. Wood mass loss data were arcsine transformed and mycelial extension data log-transformed to meet the assumptions of ANOVA. Temperature and pre-inoculated species were treated as fixed factors. Individual treatments were compared using Tukey's pairwise comparison. Effect sizes are given as omega-squared (ω^2). Effects of temperature and pre-inoculated species on CO_2 production were analysed using a GLM with a gamma distribution and a log link. Separate analyses were run for each sampling occasion. All statistical analyses were performed with R 3.4.2 (R development Core Team) except for the NMDS analyses which were performed using PC-ORD version 6 (McCune et al., 2002).

3 | RESULTS

3.1 | Initial mycelial growth of pre-inoculated fungi

Initial mycelial extension rate of pre-inoculated fungi was strongly affected by both elevated temperature ($F_{1,112} = 204.6$, $p < 0.001$, $\omega^2 = 0.44$) and species identity ($F_{7,112} = 16.6$, $p < 0.001$, $\omega^2 = 0.23$), although the magnitude of the effect of elevated temperature varied between fungal species (temperature $\times$ species; $F_{7,112} = 3.7$, $p = 0.001$, $\omega^2 = 0.04$; Table S3). For example, *F. pinicola* showed a more than fourfold increase in extension rate in elevated temperature, while *P. ferrugineofuscus* only increased its growth rate 1.7-fold (Figure 2).

FIGURE 2 Radial extension rate (mean $\pm$ *SE*) of pre-inoculated species under elevated (*n* = 8, dark bars) and normal (*n* = 8, grey bars) temperature during the first 2 weeks after inoculation. Different letters indicate significant (*p* < 0.05) differences in extension rate between assembly histories. Upper case letters refer to elevated temperatures and lower case letters to normal temperatures. Asterisks above bars indicate significant differences between temperature treatments (**p* < 0.05, ***p* < 0.01 and ****p* < 0.001)
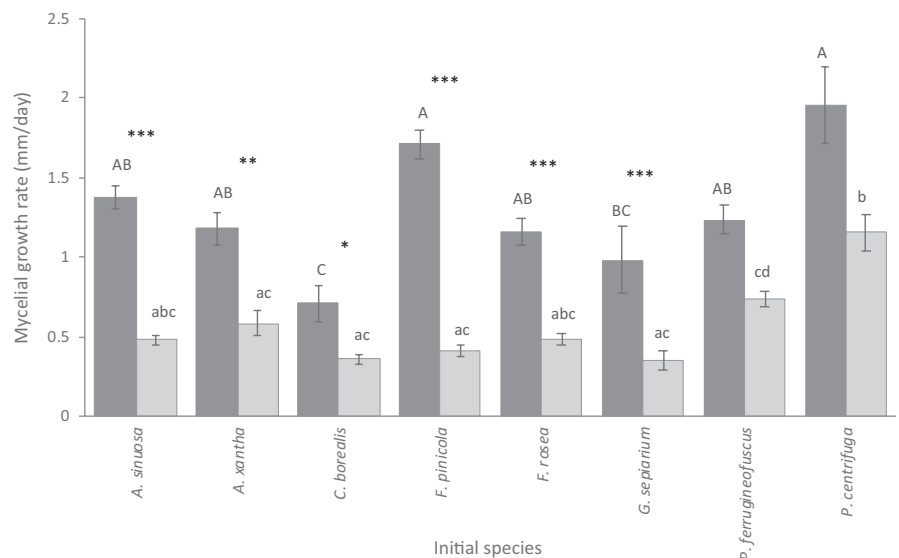
3.2 | Species composition

The multivariate GLM showed that both temperature (LRT = 45, $p < 0.001$) and assembly history (LRT = 292, $p < 0.001$) had very strong impact on community development. However, there was also a strong interaction effect, indicating that the effect of assembly history depended on temperature (temperature × history, LRT = 185, $p < 0.001$). Wood discs inoculated with the same initial species generally developed similar species composition, but for some species the distribution in the NMDS space clearly differed between normal and elevated temperature (Figure 3). For example, wood discs where *A. sinuosa* or *G. sepiarium* were introduced first showed more clearly separated communities under elevated compared to normal temperature (Figure 3a,f). In contrast, species community development initiated by *A. xantha, F. rosea* or *P. centrifuga* was less influenced by temperature (Figure 3b,e,h). *Phlebia centrifuga* was very competitive and outcompeted most other species irrespective of temperature

when introduced first, often resulting in single-species communities (Figures 3h and 4).

The final substrate occupancy of individual species was generally affected by both assembly history and temperature, although dominance analysis indicated that assembly history consistently exerted the greatest impact (Figure 4). The proportion of wood disc subsamples occupied was higher under normal temperatures for all species except *A. sinuosa, G. sepiarium* and *F. pinicola*, which showed no consistent response to temperature (Figure 4a,d,e). The overall prevalence of *C. borealis* and *F. rosea* was clearly higher under normal than elevated temperatures (Figure 4c,f). However, for *Antrodia sinuosa, A. xantha, G. sepiarium, F. pinicola, P. ferrugineofuscus* and *P. centrifuga*, there was also a strong interaction between treatments (temperature × history), indicating varied and more complex responses. For example, *P. centrifuga* had, overall, 36% higher substrate occupancy under normal temperatures, but the response depended strongly on the assembly history. When,
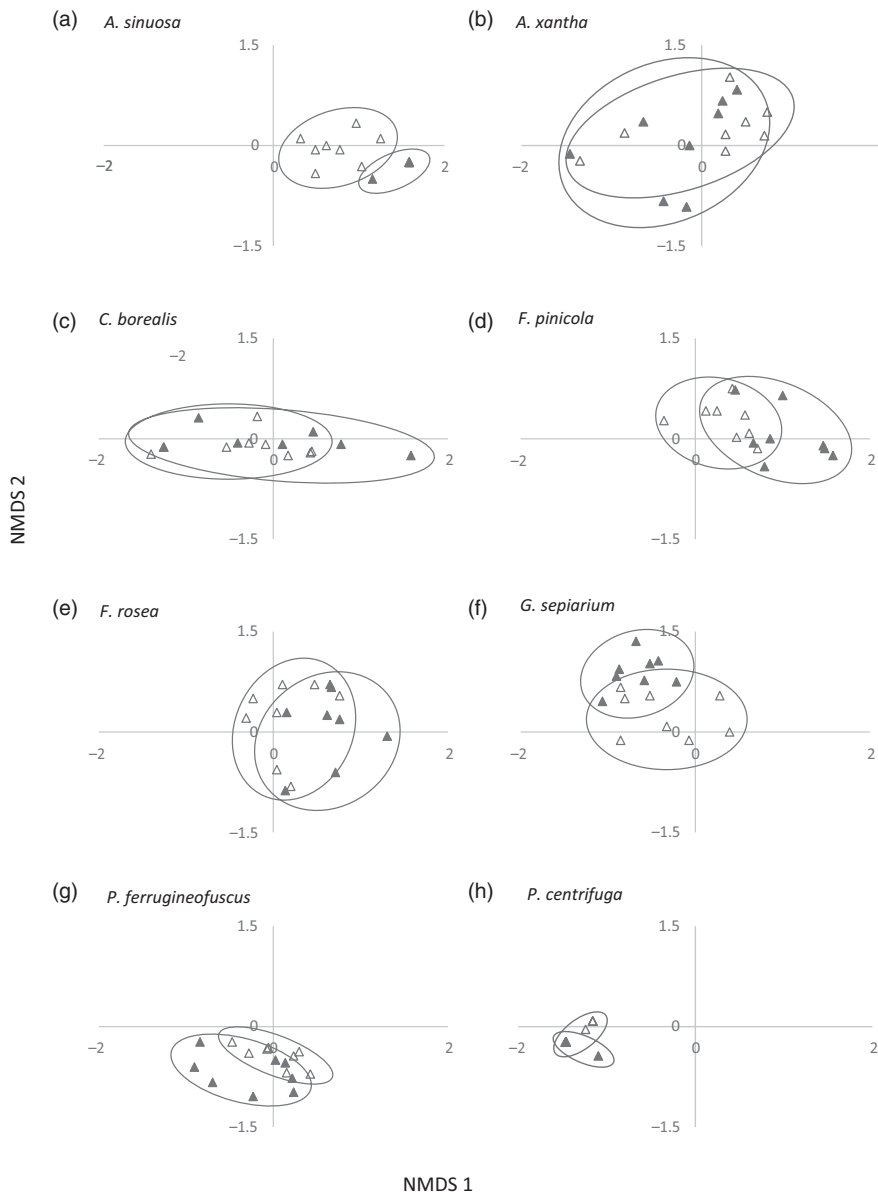

FIGURE 3 Non-metric multidimensional scaling (NMDS; stress = 0.17) of fungal community composition based on Bray–Curtis dissimilarity. Open symbols ($n = 8$) indicate normal temperature and closed symbols ($n = 8$) elevated temperature. All results originate from one analysis, but to simplify the visualization, different species are shown in separate plots (a–h). Data labels overlap in some plots

FIGURE 4 Percentage wood (mean % subsamples occupied ± SE) occupied by each species (a–h) at elevated (dark bars, n = 8) and normal (grey bars, n = 8) temperatures and with different pre-inoculated species. Since there were often more than one species occupying each subsample, total occupancy of a disc may exceed 100%. Significant (*p < 0.05, **p < 0.01, ***p < 0.001) effects of temperature (T) and assembly history (H) after model selection of individual binomial generalized linear models are indicated. Different letters indicate significant (p < 0.05) differences in substrate occupancy. For species with a significant interaction between assembly history and temperature, separate post hoc tests were performed for elevated and normal temperatures. In these cases, upper and lower case letters refer to different temperatures. Asterisks above bars indicate significant differences between temperature treatments
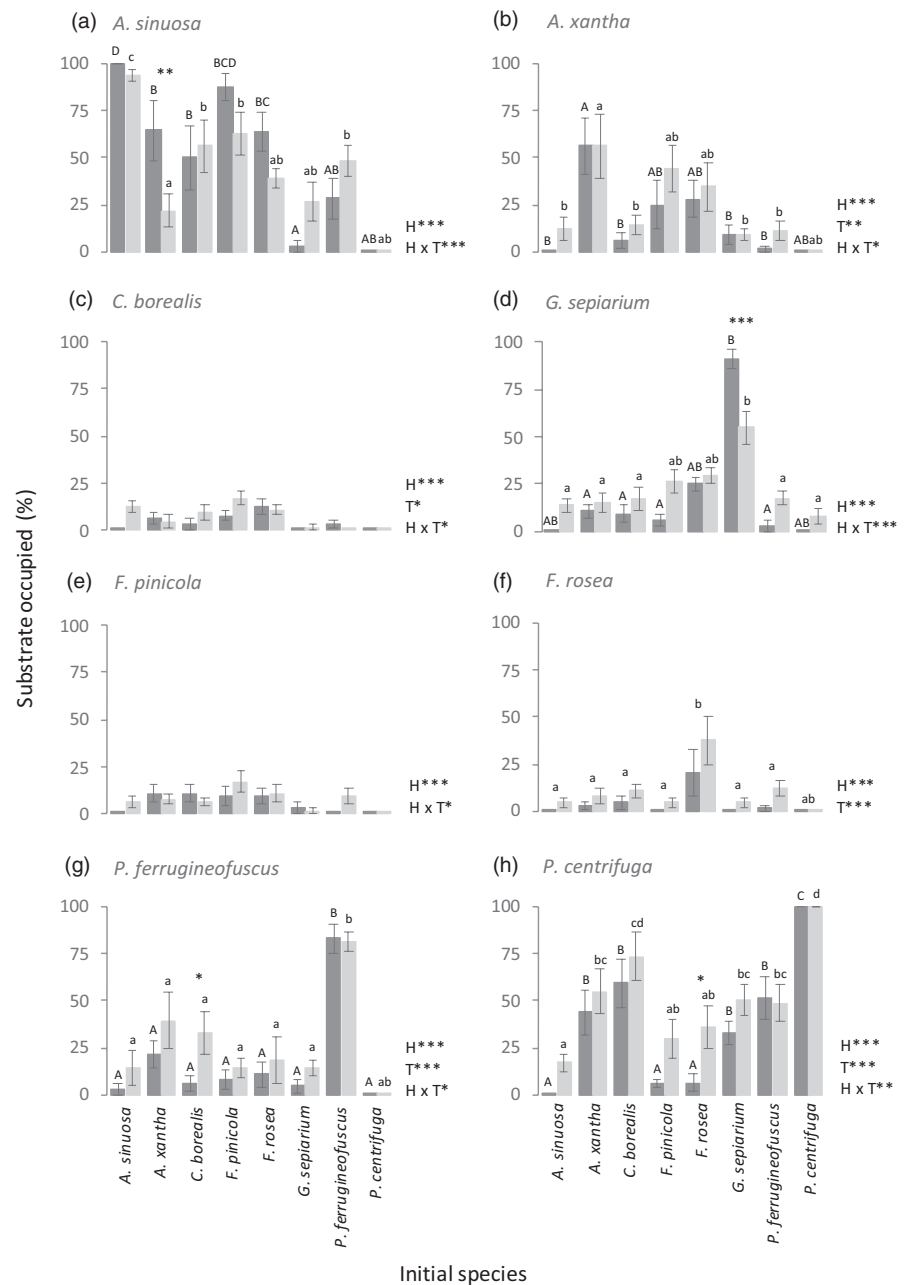
for example, *F. rosea* was pre-inoculated, the prevalence of *P. centrifuga* was almost six times higher under normal than elevated temperature, but when *P. ferrugineofuscus* was introduced first, there was no difference between normal and elevated temperatures (Figure 4h).

The advantage of arriving first affected species very differently. While, for example, *C. borealis* and *F. pinicola* showed no response, *P. ferrugineofuscus* and *G. sepiarium* were strongly favoured. *Phellinus ferrugineofuscus* occupied, on average, 82.0% and *G. sepiarium* 72.6% of the substrate at the end of the experiment when arriving ahead of other species compared to 13.4% and 13.1% otherwise (Figure 4). However, these species differed in their response to temperature when arriving first; while prevalence of *P. ferrugineofuscus* was unaffected by temperature

(Figure 4g), prevalence of *G. sepiarium* was 66% higher under elevated temperature than normal temperature (Figure 4d). Another interesting example illustrating the complexity of fungal community development in wood is the relationship between *Antrodia* and *Fomitopsis* species. Besides being favoured when introduced first, *A. xantha* and *A. sinuosa* showed high prevalence when *F. rosea* or *F. pinicola* were pre-inoculated due to a very strong competitive ability against these species. Both *F. rosea* and *F. pinicola* were inoculated on the opposite side of the disc from the *Antrodia* species (Figure 1), but in cases where they came in direct mycelial contact, *Fomitopsis* species were effectively replaced. For *F. pinicola* this resulted in low final prevalence when introduced first, even though it had the second fastest initial growth rate under warmer conditions (Figure 2; Figure 4).
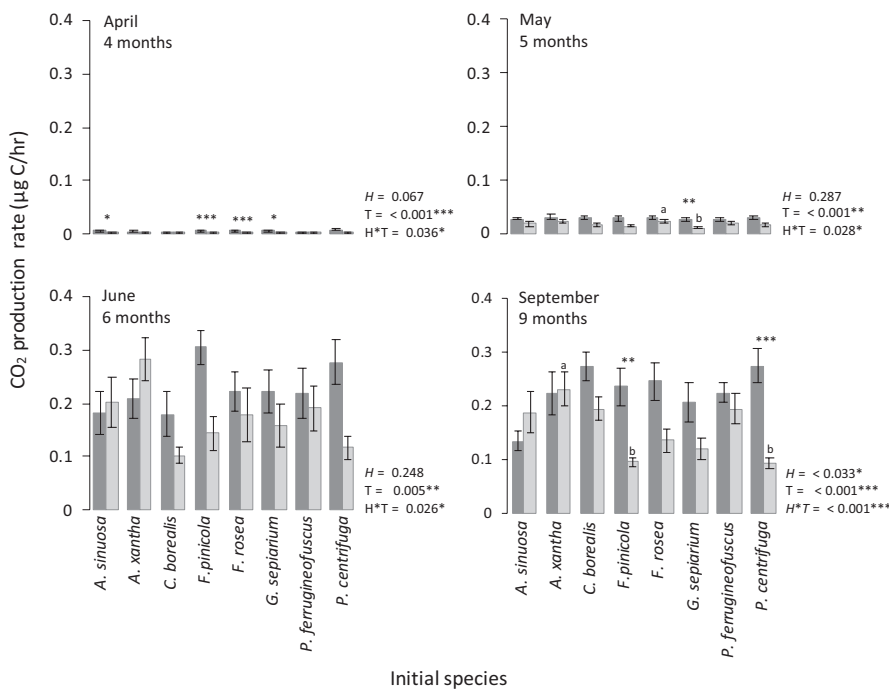
FIGURE 5 Respiration rates for all treatments over time (mean $\pm$ SE). The month represents the temperatures used (see Table S2) and the number of months indicates the time since the beginning of the experiment. Elevated temperature treatments are denoted by dark bars ($n = 8$) and normal temperatures by grey bars ($n = 8$). GLM results for the effects of assembly history (H) and temperature (T) are provided. Separate analyses were run for each sampling occasion. Different letters indicate significant (LRT, $p < 0.05$) differences in carbon release between assembly histories. Upper case letters refer to elevated temperatures and lower case letters to normal temperatures. Asterisks above bars indicate significant differences between temperature treatments (*$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$)

3.3 | Prevalence of pre-inoculated fungi

The prevalence of pre-inoculated fungi after 9 months was significantly influenced by species identity (LRT: $\chi^2(7) = 604$, $p < 0.001$, pseudo-$R^2 = 0.28$), while there was no overall effect of temperature (LRT: $\chi^2(1) = 0.26$, $p = 0.61$). However, the post hoc analysis indicated that *G. sepiarium* was clearly favoured by warming ($p = 0.0018$). In addition, there was a strong interaction between species identity and temperature (LRT: $\chi^2(7) = 36$, $p < 0.001$, pseudo-$R^2 = 0.31$), indicating that the effect of species identity on the prevalence of initial colonizers varied between temperature treatments.

Pre-inoculated species' final abundances were generally positively related to their initial growth rates, but there were exceptions. For example, *F. pinicola* had the second fastest growth rate under elevated temperatures (Figure 2), but its final abundance was the second lowest among pre-inoculated fungi (Figure 4).

3.4 | Species richness

Species richness was influenced by both temperature (LRT: $\chi^2(1) = 47.5$, $p < 0.001$, pseudo-$R^2 = 0.04$) and assembly history (LRT: $\chi^2(7) = 109.9$, $p < 0.001$, pseudo-$R^2 = 0.09$), although their interaction was also significant (LRT: $\chi^2(7) = 22.3$, $p = 0.002$, pseudo-$R^2 = 0.17$). The average number of species was 4.8 (± 2.0 SD) and 3.1 (± 1.9 SD) in normal and elevated temperatures respectively. The post hoc test showed that species richness in assembly histories initiated by *A. sinuosa* and *F. pinicola* was clearly higher under normal temperature, but no such response was found for the other assembly histories (Figure S3).

3.5 | CO$_2$ production

Both temperature and assembly history clearly affected carbon release (Figure 5). While the positive effect of warming was consistent across all four sampling occasions, the impact of assembly history was only evident after 9 months in the last measurement (September). Although elevated temperature increased the overall CO$_2$ production, there was inconsistency in the response of fungal assemblages to temperature depending on their history (temperature × history). For example, in September, temperatures in the last measurement only assemblies initiated with *F. pinicola* and *P. centrifuga* released significantly more CO$_2$ under elevated temperature compared to under normal temperature (Figure 5).

Overall carbon release was often 10–20 times higher under June and September temperatures than in April-May, reflecting lower temperatures in combination with less progress in wood decomposition in the latter. Hence, in addition to complex interactions between temperature and assembly history, the observed patterns of carbon release were highly influenced by the decay succession and monthly temperatures.

3.6 | Wood mass loss

Consistent with the carbon respiration result, warming had considerable impact on wood decomposition and increased mass loss across all assembly histories ($F_{1,112} = 41.02$, $p < 0.001$, $\omega^2 = 0.21$; Figure 6; Table S4). Average mass loss was 14.5% under normal temperature compared to 19.4% under elevated temperature, representing 34% higher mass loss under warming. Mass loss ranged from 12% in discs where *C. borealis* was introduced first under normal temperature

FIGURE 6 Percentage wood mass loss (mean ± SE) under elevated (dark, $n = 8$) and normal (grey, $n = 8$) temperature treatments. The pre-inoculated species are indicated under the bars. Different letters above bars indicate significant ($p < 0.05$, ANOVA, Tukey's HSD) differences in loss of wood mass between assembly histories. Upper and lower case letters refer to different temperature treatments. Asterisks indicate significant differences between temperature treatments (*$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$)
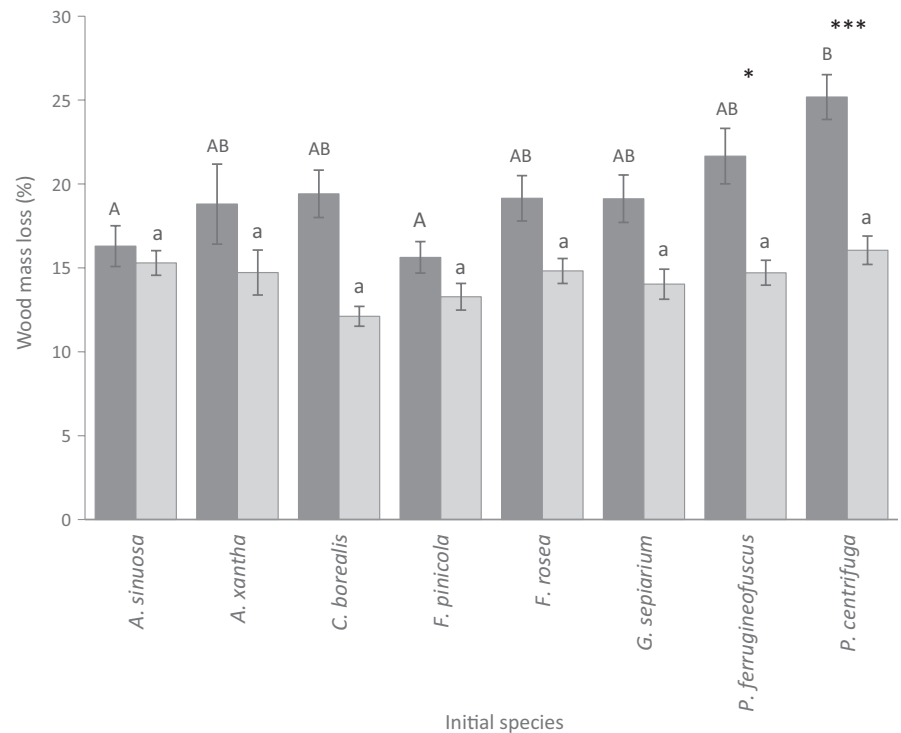
to 25% in discs were *P. centrifuga* was introduced first in elevated temperature. Although temperature was the factor exerting greatest influence on decomposition, it was also affected by assembly history ($F_{7,112} = 3.52$, $p < 0.01$, $\omega^2 = 0.09$; Figure 6). However, there was also an interaction between assembly history and temperature ($F_{7,112} = 2.10$, $p < 0.05$, $\omega^2 = 0.03$), and separate analyses at normal and elevated temperatures revealed that assembly history was only significant under warmer conditions. Assemblies initiated by *P. centrifuga* at elevated temperatures experienced a loss of mass 1.6 times higher (25%) than assemblies initiated by *F. pinicola* (16%) and *A. sinuosa* (16%; $F_{7,56} = 4.26$, $p < 0.001$; Figure 6). In addition, when *P. centrtifuga* was introduced first, warming increased mass loss by 57%, compared to an increase of only 7% when *A. sinuosa* was introduced first. Hence, the relative response to warming was eight times higher in *P. centrifuga* histories compared to *A. sinuosa* histories.

Wood mass loss was negatively correlated with fungal species richness, although the explained variation was low ($R^2 = 0.13$, $F_{(1,126)} = 18.8$, $p < 0.001$; Figure S4).

4 | DISCUSSION

Previous work on decomposition dynamics reveals that both temperature and fungal assembly history are major drivers of decay rates and species community development in wood (Fukami et al., 2010; Hiscox, Clarkson, et al., 2016). However, the combined effect of these factors on decay dynamics has, to our knowledge, never been studied previously. Here we extend current knowledge by showing that temperature and assembly history jointly influence decomposition, respiration and fungal community development in wood.

Depending on which species colonized first, an average warming of 5.4°C increased decomposition by 7%–57%. The large variation in decomposition in response to warming reflects species-specific responses in growth and competitive ability of initial colonizers, resulting in different community composition. Hence, communities that caused high wood mass loss in response to warming were probably dominated by species whose decay capacity were favoured under elevated temperature. This is in line with previous studies showing that thermal optima for mycelial growth differ between species and that even small changes in temperature have the potential to alter fungal interactions in wood (A'Bear, Murray, et al., 2013; Crowther et al., 2012; Hiscox, Clarkson, et al., 2016).

However, in addition to these direct effects in species physiological response to warming, indirect effects, such as differences in the allocation of resources between decomposition and antagonistic interactions, may be involved. In wood fungal communities, investment in resource competition is costly, and decomposition rates generally decrease with increasing density of competitors (Hiscox, Savoury, Vaughan, et al., 2015; Maynard et al., 2017). This relationship was also found here, although the explained variation in mass loss was low. Assemblies subjected to warmer conditions had, in general, fewer species left at the end of our experiment. It is, therefore, likely that reduced interspecific competition contributed to the faster decomposition under elevated temperatures. The lower species richness at elevated temperatures is probably caused by species' metabolism and competition strength being higher when conditions are warmer, resulting in competitive exclusions and species succession occurring at a faster rate. In addition, some initial colonizers captured more wood resources under warmer conditions and thereby increased the competitive exclusion of late arriving species.

Although the potential for climate warming to alter fungal communities is well established (Romero-Olivares et al., 2017), this is the first study to show that community composition in wood is affected by the combination of temperature and assembly history. This can be illustrated by communities where *G. sepiarium* was introduced first. Although *G. sepiarium* influenced community development in both normal and elevated temperatures, they were more distinctly different from other communities under warming. *Gloeophyllum sepiarium* is well known to benefit from elevated temperatures (Schmidt, 2010) and is common on conifer wood in sun-exposed environments (Edman & Jonsson, 2001). Here it was strongly favoured under elevated temperatures when arriving ahead of the other species, resulting in strengthened priority effects on community composition.

One factor that evidently can be important for the success and impact of initial colonizers is their initial growth rate. The mycelial extension rate of initial colonizers was strongly species-specific and in several cases positively related to their long-term abundance in wood. Fast growing species like *P. centrifuga* and *A. sinuosa* generally dominated the communities after 9 months when introduced first (inhibitory priority effects), while slow-growing species such as *C. borealis* were less influential. This suggests that rapid growth is an important determinant of the strength of priority effects, which is in agreement with previous research showing that early colonizers with a fast growth rate tend to have a competitive advantage and stronger influence on community development (Cline & Zak, 2015; Vannette & Fukami, 2014; Vaughn & Young, 2015). The advantage of rapid growth probably lies in the fact that the fungus is able to capture a larger domain before encountering other competing mycelia in a new wood resource. Previous research has shown that the size of fungal domains is an important determinant of interaction outcomes between wood-decaying fungi (Holmer & Stenlid, 1993). Further, a larger domain is likely to be more persistent over time with more pronounced chemical and physical modifications to the wood, making conditions less optimal for potential invaders (Hiscox, Clarkson, et al., 2016).

Although rapid growth resulted in increased final domains in several pre-inoculated species, there were exceptions, and only *G. sepiarium* was clearly favoured under warming despite increased growth rates in most species. For example, the growth rate of *Fomitopsis pinicola* was the second fastest at elevated temperatures, but still it captured very small domains in the end. In this case we observed that rapid mycelial expansion resulted in direct contact with *Antrodia* species on the opposite side of the wood disc, which resulted in more or less complete replacement of *F. pinicola* due to its low competitive ability against these species. Here, fast extension rate of the initial species promoted secondary colonizers (facilitative priority effect) and larger final domains of the initial species were captured under normal temperatures and slower growth. This highlights the importance of species-specific competitive traits and species' spatial arrangement in wood for outcomes of interactions and community development, which has previously been demonstrated experimentally (Hiscox et al., 2018). Further, allocating resources to rapid growth and competition may come at the expense of other life-history or physiological traits, such as stress tolerance. Fungi with fast extension rates and high competitive abilities generally have a smaller niche width than species with slow extension rates and low competitive abilities (Maynard et al., 2017). Hence, species with rapid growth may be more sensitive to changes in environmental conditions, such as under climate warming, resulting in a dampening of priority effects.

Priority effects on community composition and decomposition have been suggested to be strongest in the early stages of succession and weaken in later stages as decay progresses (Dickie et al., 2012; Hiscox, Savoury, et al., 2016). According to our respiration data, effects of assembly history were strongest after 9 months, that is, in the last measurement. Although the progress of decay was quite advanced, with up to 25% dry mass loss in some histories (fungal biomass included), it is possible that the strength of priority effects would have declined if the experiment had run longer. Hence, it is important to point out that our results represent the early- to mid-decay succession when priority effects are expected to be strongest.

Although we found a strong interaction between temperature and assembly history, the extent to which this applies to natural systems remains uncertain. For example, under natural conditions, the temperature is not constant, but fluctuates over the day. Toljander et al. (2006) found that fluctuating temperatures facilitate a higher species richness compared to a constant temperature. However, the temperature buffering capacity of logs is high (Carlsson et al., 2012), which probably reduces diurnal temperature variability within wood, especially in large pieces. Nevertheless, diurnal temperature fluctuations may affect the strength of priority effects and their interaction with temperature and therefore deserves further investigation.

Microcosm experiments are often useful for identifying important mechanisms and causal relationships in ecological processes that are difficult to test in nature (Drake & Kramer, 2012). However, the simplified approach has its limitations. In our experiment, the only environmental factor included was temperature. Under natural conditions, climate warming is accompanied by changes in many other factors, both biotic and abiotic, as well as their interactions. Perhaps most important, climate change results in altered precipitation patterns and greater evaporation. Such changes will influence the water regime within wood and soil, with consequences for fungal community composition and decomposition. For example, the stimulating effect of warming on decay rates may not occur in areas also affected by drought, where increased evapotranspiration may reduce moisture content to the point where fungal decomposition is inhibited (Christiansen et al., 2017).

It is also unclear how well our artificial inoculation mimics colonization in natural systems where colonization pathways are more complex. For example, our experiment involved only a limited set of species. Under natural conditions, a wide range of fungal species have the potential to colonize the wood. Hence, more species may establish themselves and different fungal communities may be selected for under normal and elevated temperatures, with consequences for respiration and decomposition rates. On the other hand, Dickie et al. (2012) showed that fungal assembly history can have strong effects on ecosystem properties even under natural levels of environmental variability, and theory predicts that priority effects

become even more important as the number of potential colonizers increases (Chase, 2003).

5 | CONCLUSIONS

The Intergovernmental Panel on Climate Change (IPPC) predicts that, over the course of the 21st century, mean temperatures will increase by 2–8°C in in the boreal region (IPCC, 2013). This will clearly have consequences for boreal carbon storage, although the magnitude is uncertain given the complex nature of decay dynamics. A key to understanding this process is gaining more knowledge about how climate factors interact with other abiotic and biotic factors, which may enhance or dampen effects of climate change. Here we present evidence that warming effects on wood decay depend on fungal assembly history. An elevated temperature of 5.4° resulted in species-specific responses of early colonizers with consequences for community composition and decomposition. Although decay rates increased in all histories under warmer conditions, the variation in response was profound. However, it is important to stress that our findings result from controlled laboratory conditions and cannot be translated into natural conditions. It remains for future work to confirm our findings under natural conditions, where multiple abiotic and biotic factors regulate saprotrophic fungal community composition and function.

AUTHORS' CONTRIBUTIONS
M.E. conceived the ideas and designed the experimental setup together with S.H.; S.H. and M.E. collected and isolated the fungal species; S.H., M.E. and F.C. performed the experiment; F.C. designed primers and ran pcr analyses; M.E. and S.H. performed statistical analyses and wrote the manuscript.

DATA AVAILABILITY STATEMENT
Data are archived and available from Mid Sweden University: http://urn.kb.se/resolve?urn=urn:nbn:se:miun:diva-40848 (Edman, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.