Independent effects of host and environment on the diversity of wood-inhabiting fungi

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Abstract
1. Dead wood is a habitat for numerous fungal species, many of which are important agents of decomposition. Previous studies suggested that wood-inhabiting fungal communities are affected by climate, availability of dead wood in the surrounding landscape and characteristics of the colonized dead-wood object (e.g. host tree species). These findings indicate that different filters structure fungal communities at different scales, but how these factors individually drive fungal fruiting diversity on dead-wood objects is unknown.

2. We conducted an orthogonal experiment comprising 180 plots (0.1 ha) in a random block design and measured fungal fruit body richness and community composition on 720 dead-wood objects over the first 4 years of succession. The experiment allowed us to disentangle the effects of the host (beech and fir; logs and branches) and the environment (microclimate: sunny and shady plots; local dead wood: amount and heterogeneity of dead wood added to plot).

3. Variance partitioning revealed that the host was more important than the environment for the diversity of wood-inhabiting fungi. A more detailed model revealed that host tree species had the highest independent effect on richness and community composition of fruiting species of fungi. Host size had significant but low independent effects on richness and community composition of fruiting species. Canopy openness significantly affected the community composition of fruiting species. By contrast, neither local amount nor heterogeneity of dead wood significantly affected the fungal diversity measures.

4. Synthesis. Our study identified host tree species as a more important driver of the diversity of wood-inhabiting fungi than the environment, which suggests a host-centred filter of this diversity in the early phase of the decomposition process. For the conservation of wood-inhabiting fungi, a high variety of host species in various microclimates is more important than the availability of dead wood at the stand level.
INTRODUCTION

Many fungal species inhabit dead wood, where they are important agents of decomposition and associated fluxes of carbon and nutrients (Bradford et al., 2014; Floudas et al., 2012). Although the global number of fungal species living on dead wood is unknown (Boddy, Frankland, & Van West, 2007), a review study covering Norway, Sweden and Finland documented that more than 2,500 species associated with dead wood exist in this area (Stenlid, Penttilä, & Dahlberg, 2008). On a single dead-wood log, at least 46 fruiting species can coexist (Heilmann-Clausen & Christensen, 2004). Despite the importance and diversity of wood-inhabiting fungi, our understanding of the factors driving the spatial and temporal patterns of their diversity is limited. It has been suggested that characteristics of the colonized dead-wood object (host) and the environment surrounding an object are important drivers of the diversity of wood-inhabiting fungi (Heilmann-Clausen et al., 2016; Seibold, Bässler, Brandl, et al., 2016; Seibold et al., 2015 and therein). However, how the host and the environment individually affect fungal diversity on dead-wood objects is unknown (Bradford et al., 2014). Untangling and comparing the importance of host vs. environmental drivers would yield basic ecological knowledge about wood-inhabiting fungal communities and allow predictions about the influence of silviculture on this important group of fungi in forest ecosystems.

Numerous studies have shown that the host affects the diversity of wood-inhabiting fungi (Baber et al., 2016; Hoppe et al., 2015; Kahl et al., 2017). The host is the resource and provides energy for metabolism, growth and reproduction (Stokland, Siitonen, & Jonsson, 2012), which can be depleted (Field, Chapin, Matson, & Mooney, 1992). The host is also the habitat, which is characterized by specific conditions, for example, pH, moisture and composition of carbon compounds. Especially the host tree species and the size of dead wood are important drivers of fungal diversity (tree species: Baber et al., 2016; Ferrer & Gilbert, 2003; Nordén, Ryberg, Götmark, & Olausson, 2004; tree size: Heilmann-Clausen & Christensen, 2004; Juutilainen, Halme, Kotiranta, & Mönkkönen, 2011). Physicochemical properties differ between host species, especially between gymnosperms and angiosperms (Brunow, 2005; Higuchi, 2006), and this difference should contribute to explain differences in the composition of fungal communities (e.g. Hoppe et al., 2015; Kahl et al., 2017).

Furthermore, physicochemical properties and hence habitat conditions change over time and are caused by biotic activity of fungal primary (endophytes) and secondary colonizers (e.g. changes in the composition of carbon compounds, e.g. Hoppe et al., 2015) or non-fungal saprophytic organisms (Saint-Germain, Drapeau, & Buddle, 2007). Both groups of colonizers can affect the colonization success of species arriving later—the so-called “priority effect” (Dickie, Fukami, Wilkie, Allen, & Buchanan, 2012; Fukami et al., 2010; Hiscox, Clarkson, et al., 2016; Hiscox, Savoury, et al., 2016; Song, Kennedy, Liew, & Schilling, 2017; Song, Vail, Sadowsky, & Schilling, 2015). With regard to the size of a dead-wood object, a log provides more resources in space and time for fungi than a branch (Heilmann-Clausen & Christensen, 2004; Juutilainen et al., 2011). Furthermore, logs and branches differ in their anatomical, chemical and physical properties, for example, the presence of heart wood (Jacobson, Rademacher, Meesenburg, & Meiwees, 2003). Therefore, different wood-inhabiting fungal species could prefer different niches represented by different species and sizes of dead-wood objects (Juutilainen et al., 2011).

Beside host properties, the environment of a dead-wood object affects fungal diversity. Among environmental conditions, stand microclimate and the amount and heterogeneity of dead wood in the surroundings seem to be of particular importance. First of all, numerous studies have shown that the diversity of wood-inhabiting fungi is correlated with canopy openness—a proxy for microclimate conditions (Bässler et al., 2016; Bässler, Müller, Dziock, & Brandl, 2010; Horák, Kout, Vodka, & Donato, 2016; Lehnert, Bässler, Brandl, Burton, & Müller, 2013). This correlation is not surprising as forest gap dynamics caused by anthropogenic disturbances, for example, logging, or natural disturbances, for example, windthrows, insects, fire or snow, is an important driver influencing the diversity of forest species across numerous taxa at the landscape scale (Swanson et al., 2011). Variation in canopy openness is physically correlated to changes in moisture and temperature regimes and to fluctuations of these variables also within a dead-wood object (Scharenbroch & Bockheim, 2007; Seibold, Bässler, Brandl, et al., 2016). Variation in microclimate within dead wood can therefore have pronounced effects on the fungal community (Boddy & Heilmann-Clausen, 2008; Pouska, Macek, Zibarová, & Ostrow, 2017). However, current results are inconsistent, and both negative (Bässler, Müller, et al., 2010; Horák et al., 2016) and neutral effects (Bässler et al., 2016) of the microclimate on species richness have been reported. Second, the amount and heterogeneity (e.g. different host tree species) of dead wood at and around the stand can effect source populations of fungi (Edman, Kruys, & Jonsson, 2004; Nordén, Penttilä, Siitonen, Tomppo, & Ovaskainen, 2013; Nordén et al., 2004; Norros, Penttilä, Suominen, & Ovaskainen, 2012). For example, when the amount of dead wood in a forest stand is high, we would expect that more individuals occur in an area owing to the larger dead-wood area (species pool, species-area relationship, MacArthur & Wilson, 1967). Consequently, more species would be found on a nearby object because of increased colonization events due to dense spore rain near existing fruit bodies (e.g. "random replacement hypothesis" Coleman, Mares, Willig, & Hsieh, 1982). This view is supported by
Edman et al. (2004), who showed that the number of fungal species on freshly cut logs was higher on sites with large local amounts of dead wood than on sites with small amounts. The mechanism behind this pattern has been attributed to differences in donor populations caused by differences in resource availability. However, it is not possible to infer from observational studies a causal relationship between dead-wood amount and fungal diversity because under natural conditions, the amount and heterogeneity of dead wood are often correlated (Müller & Büttler, 2010; see also “habitat amount hypothesis” Fahrig, 2013). By contrast, other studies observed no differences in the fungal diversity pattern on objects exposed to different amounts of dead wood in the surroundings (Olsson, Jonsson, Hjältén, & Ericson, 2011; Rolstad, Sætersdal, Gjerde, & Storaunet, 2004). In these cases, drivers other than dead-wood amount (e.g., abiotic environment) might have driven the fungal diversity pattern on the logs.

Despite these numerous observational studies of the drivers of the diversity of wood-inhabiting fungi, the relative importance and interaction of the host and environment remain unclear. This lack of knowledge prohibits a deeper understanding of how fungal communities are structured and limits our ability to take measures to maintain fungal diversity and related processes in managed forest ecosystems. Therefore, we set up an orthogonal experiment in which we varied the host and the environment. The host was varied by adding dead wood of different species (fir or beech) and of different size (branches or logs); the environment was varied by varying the stand microclimate (sunny plots in forest gaps or plots under shady canopies) and by varying the local dead wood by adding dead wood in high or low amounts and of low, middle or high heterogeneity (for definitions, see Table 1). We considered the number of fruiting species of fungi (hereafter “number of species”) and the community composition of fruiting species (hereafter “community composition”) on dead-wood objects as response variables and addressed the question: Is the host (species and size) more important for fungal diversity than the environment (stand microclimate and local dead wood)?

### Table 1: Definition of the main variables with their description, measurement and ecological meaning. We defined five variables in two sets of variables

| Variable sets | Variable | Description | Measurement | Ecological meaning |
|---------------|----------|-------------|-------------|--------------------|
| Host          | Host size| Size of a dead-wood object | Branches (fine woody debris); logs (coarse woody debris) | Resource availability, habitat (micro-environment) |
|               | Host species | Tree species of a dead-wood object | Fagus sylvatia (beech); Abies alba (fir) | Habitat (micro-environment) |
| Environment   | Stand microclimate | Proxy for microclimate conditions on the plot level | Canopy openness (sunny, shady) | Macro-environmental climate stand level |
| Local dead-wood amount | High and low amount of dead wood added to the plot | Surface (m²) | Species pool size |
| Local dead-wood heterogeneity | Gradient of dead-wood diversity added to the plot | Siitonen index (low, middle, high) | Species pool diversity |

### 2.1 Study area and experimental design

The experiment was conducted in the management zone of the Bavarian Forest National Park in south-eastern Germany. The management zone covers an area of c. 6,000 ha around the c. 18,000 ha core zone. The former is characterized by montane mixed forest consisting of Norway Spruce (Picea abies (L.) H. Karst), European Beech (Fagus sylvatica L.) and Silver Fir (Abies alba Mill.) (Bässler, Stadler, et al., 2016). Overall, 180 plots of 0.1 ha were arranged in a random block design of five blocks (Figure S1). In autumn 2011, we freshly cut and directly deposited (within less than 8 weeks) c. 7,400 dead-wood objects of four different types: logs (coarse woody debris; mean diameter ± 5D = 33 ± 6.5 cm, length = 5 m) and branches (fine woody debris; mean diameter ± 5D = 3.2 ± 1.3 cm, mean length ± 5D = 2.7 ± 0.88 m) of beech and fir. The wood objects were taken from trees of the same age that were harvested from the same forest stand. Each plot contained either fine or coarse woody debris or both and either beech or fir or both (Figure S1; see also Seibold, Bässler, Baldrian, et al., 2016; Seibold, Bässler, Brandl, et al., 2016), creating three levels (low, middle and high) of dead-wood heterogeneity. The lowest level comprised either logs or branches of beech or fir; the intermediate level comprised logs and branches of beech or fir, or logs or branches of beech and fir; and the highest level comprised logs and branches of beech and fir (Figure S1). Half of the plots contained a low amount of local dead wood (8 branches of c. 0.2 m²/ha or 4 logs of c. 10 m²/ha) and the other half contained a high amount of local dead wood (80 branches of c. 2 m²/ha or 40 logs of c. 100 m²/ha). We used canopy openness as a surrogate for stand microclimate (Müller et al., 2015; Seibold, Bässler, Brandl, et al., 2016; Vodka, Konvicka, & Cizek, 2009) and created each combination of dead-wood amount and heterogeneity twice per block, once in a sunny gap and once under a shady canopy (Figure S1). The sunny gaps are a result of clearings; an area of 0.1 ha was freed from living or dead trees. Penetration rates of
airborne LiDAR (light detection and ranging) differed considerably between sunny and shady plots (c. seven-fold) on an area of 0.5 ha (Figure S2). To avoid shading by a dense grass layer surrounding the logs and branches on sunny plots, each plot was mowed once a year during the growing season (for details, see Seibold, Bässler, Baldrian, et al., 2016; Seibold, Bässler, Brandl, et al., 2016).

We calculated an index of local dead-wood heterogeneity as the number of different substrate types per plot, ranging from low to high (according to the above classification of the heterogeneity set-up; Siitonen, Martikainen, Punttila, & Rauh, 2000; see Figure S1). To precisely characterize the amount of dead wood per plot, we calculated the surface area of each object using the formula for a truncated cone and summed the surface area of all logs and branches and of the sampled objects separately (see below). Surface area was calculated from the length and diameters measured on both ends of each object. We considered surface area as recommended by Heilmann-Clausen and Christensen (2004) because we sampled fruit bodies on the surface of dead-wood logs and branches and because the surface of an object basically reflects the number of arriving propagules; objects with larger surfaces are more likely to be reached by a spore (airborne dispersal) or mycelium (soilborne dispersal), as suggested by Edman et al. (2004) and in theory by the random replacement hypothesis leading to a species-area relation-ship (Coleman et al., 1982).

2.2 | Fruit body sampling

We sampled fruit bodies on a subset of two logs and four branches on each plot three times per year for four consecutive years (2012–2015), which led to a total of 720 sampled objects (hosts). The first campaign of each year was in spring (April/May), the second in summer (July/August) and the third in autumn (September/October), the main season of fruit body development. Fruit bodies were identified in the field or, if necessary, in the laboratory with the aid of a microscope. Voucher specimens were deposited in the herbarium of the Bavarian Forest National Park. The nomenclature followed MycoBank (Crous et al., 2004; see Table S1 for the complete list of species). We considered all visible species, in contrast to other studies, which restricted investigated fruit bodies to a size threshold of >1–5 mm (Nordén et al., 2004) or 10 mm (Ódor et al., 2006) or to a taxonomic group, for example, polyporoid fungi (Junninen, Penttilä, & Martikainen, 2007). A threshold of 1 mm would exclude some of the smallest sporocarps that we observed, for example, Hamatocanthoscypha laricionis (Velen.) Svrcek (145 records), whose fruit bodies do not exceed 0.5 mm (Huhtinen, 1990).

To ensure an effective and non-redundant sampling, we divided logs into seven sectors, two representing the cut edges of the log and five representing the trunk surface (each 1 m long), and sampled fruit bodies within each sector. Each branch was considered as one sector. Based on these data, we calculated a community matrix, within which the abundance of a species on an object is the sum of occupied sectors, summed across the three campaigns per year.

2.3 | Statistical analysis

To approach our study question, we first used variance partitioning to test for overall effects of host and environment on the number of species and community composition. Then, we used a serial model framework to disentangle the individual effects of all main predictors and their interactions on richness of species (for definition see below) and community composition by accounting for sampled surface. For the latter step, we used three approaches: (1) linear mixed effects and generalized linear mixed-effects models for the response variable number of species; (2) linear mixed-effects models for the first four axes of a correspondence analysis (LME-CA) and (3) ANOVA-like permutation tests for constrained correspondence analysis (ANOVA-CCA). The ANOVA-CCA integrates the full ordination space (all axes), but does not consider the nested design of our study. By contrast, the LME-CA analysis accounts for the nested design of our study by integrating a random effect.

2.3.1 | Data preparation

First, we calculated the number of species for each object and year. This measure was closely correlated with the total abundance on this object of the respective year (sum of the sectors for each object and year summed over three campaigns, adjusted $R^2 = .84$, $p < .001$; both were log$_{10}$-transformed; Figure S3, see also above for the definition of species abundance on an object). Second, we considered the community composition and used abundance data (square-root transformed) and presence/absence data. We considered only species that occurred on at least five objects in a respective year, and to generate robust communities, we considered only objects with at least three species in a respective year. To increase the explained variance of our final model (described below), we empirically tested the influence of species that occurred on at least one to six objects in a year and compared the explained variance ($R^2$) of our final CCA models. This exercise showed that inclusion of species that occurred on at least five objects within a particular year yielded the highest $R^2$ value; we used this threshold for all subsequent analyses. To test whether the excluded rare species had any effect on our interpretation, we compared the reduced community matrices with the full community matrix based on procrustes rotation using the function protest in the R package vegan. All $R^2$ values of the comparisons were above .99; thus, rare species did not significantly affect our analysis.

2.3.2 | Variance partitioning

To assess overall effects, we partitioned the variance in the response variables number of species and the community composition between (1) the host set (host species and host size) and the environmental set (stand microclimate, local dead wood), considering year as a covariate. We calculated the individual fractions of the variables sets using partial (linear) regression (Peres-Neto, Legendre, Dray, & Borcard, 2006) for the number of species using the function varpart in the R package vegan (Oksanen, 2015). For community
composition, we used partial CCA using the function cca in the R package vegan. We report the adjusted $R^2$ values for individual effects (fractions explained uniquely by each of the two sets and year as covariate) scaled to 100%.

### 2.3.3 Models for the number of species

To assess the main and interacting effects of each predictor on the number of species, we constructed a series of models. Our first model, which we termed the “sample model” (Table 2), included the factorial predictors year and size (logs or branches) and the interacting relationship between year, size, and the log$_{10}$-transformed sampled surface (i.e. the surface area of the sampled logs and branches). This model showed significant interactions between size and sampled surface across years (Figures 2 and 3). We therefore decided to include an interaction term that considered year, size and sampled surface as a covariate in all subsequent models. This approach allowed us to interpret species numbers as species richness because the models accounted for sampling effort (surface) (Gotelli & Colwell, 2011). We therefore used the term “species richness” in cases where we controlled for sampling effort in the models.

In the second model, that is, the “basic model” (Table 2), we added treatment variables (host species, canopy openness, local dead-wood amount and local dead-wood heterogeneity) to the sample model. Based on this model, we systematically checked for interactions among all two-way combinations of predictors, that is, canopy openness, host species, host size, local dead-wood amount, local dead-wood heterogeneity and year. We iteratively added one of the two-way interactions to the basic model and tested for a significantly better fit of the model using the function anova within the R package stats. If the model with the new interaction yielded a significantly better fit (based on the chi-squared test, as we used models with Poisson error) than the basic model, we added this interaction to the final model.

Our third, “final model” then consisted of the basic model and significant interacting effects (Table 2). We considered only two-way interactions to reduce complexity. We used linear mixed-effects models using the functions lmer/glmer within the R package lme4 (Bates, Maechler, Bolker, & Walker, 2015). Each model contained “object” nested within “plot” nested within “block” as random effect to account for the nested design and repeated sampling of objects. The number of species is a count variable; therefore, a statistical model using the Poisson error distribution with a log-link function would be an appropriate choice (generalized linear mixed-effects model, GLME). As the results of such models showed over-dispersion, we included a random variable to account for individual-level variability (Elston, Moss, Boulinier, Arrowsmith, & Lambin, 2001). In all models that included such an individual-level factor, the algorithm for estimating the model failed to converge. Therefore, we log$_{10}$-transformed the number of species and used a linear mixed-effects model (LME). Solutions of the GLME and LME were consistent (Table 3, Table S2). For all comparisons within and among the models, we used standardized effect sizes of the parameter estimates with an expected mean of 0 ($z$ values $=$ estimates divided by the respective standard error; see Bring, 1994), and $p$ values were inferred using the R package multcomp (Hothorn, Bretz, & Westfall, 2008). Note that we tested for interactions independent of the significance of main effects as significant factorial interactions can be meaningful without overall significant effects of the individual factors (“crossover interactions,” e.g. VanderWeele & Knol, 2014).

### 2.3.4 Models for the community composition

As outlined above, we used two approaches (LME-CA and ANOVA-CCA) to address the main and interacting effects of the predictor variables on the community composition as a response. For the first approach (LME-CA), we subjected the final community matrix to a CA using the function cca in the R package vegan (Oksanen, 2015). We used the scores of the first four CA axes for further analysis. We also used presence/absence data to calculate the CA (results not shown) and found a high consistency with the abundance-based results. This consistency was not surprising as we found a strong relationship between these two correspondence analyses ($R^2 = .96$, $p < .001$, permutations = 9999, based on procrustes rotation with the function protest from R package vegan). Using the scores of the first four axes from the CA, we applied the same model framework as for the number of species (see above). As the derived axes from the CA ordination were normally distributed, we used LMEs for these models. Using scores of the CA axes within the LME-CA framework allowed us to specify a random effect to account for the

| Model       | Description                                                                 | Predictors                                                                 |
|-------------|------------------------------------------------------------------------------|----------------------------------------------------------------------------|
| Sample      | Check for co-variation of year, size and sampled surface                      | Year + host size + year: host size: sampled surface + (1|block/plot/object)  |
| Basic       | Added treatment variables and systematically checked for interactions among all predictors | Year + host size + year: host size: sampled surface + (1|block/plot/object) + host species + local amount + local heterogeneity + canopy openness |
| Final       | Sample model and all variables with significant interactions (tested in basic model) estimated as overall and interacting effects | Example: year + size + year: host size: sampled surface + (1|block/plot/object) + significant interactions |
nested design of our study. However, to consider the full ordination space, we fitted in a second approach (ANOVA-CCA) the same series of models (sample, basic and final) as described above using the function *cca* in the *r* package *vegan* and used ANOVA-like permutation tests for CCA to test for significance of predictors and interactions (function *anova.cca* within the *r* package *vegan*).

We interpreted effects as significant in our study if effects were significant across statistical approaches (for species richness LME and GLME; for the community composition LME-CA and ANOVA-CCA).

### RESULTS

A total of 45,992 sectors were occupied by at least one fungal species (we considered an occupied sector as a record). The number of records increased with succession (2012: 3,880; 2013: 9,124; 2014: 15,837 and 2015: 17,151). Across all records, we found 291 species of fungi, including 116 species of Ascomycota and 175 species of Basidiomycota. The most common basidiomycete species was *Cylindrobasidium leave* (Pers.), and the most abundant ascomycete species was *Hypoxylon fragiforme* (Pers.) J.Kick.x.f. (for the rank-abundance curve and the 20 most abundant species, see Figure S4).

The set of host variables (host species, host size) clearly explained more of the partitioned variance of number of species and community composition than the environment (stand microclimate, local amount and local heterogeneity of dead wood, Figure 1).

### 3.1 | Species richness

The relationship between the number of species and the sampled surface differed between the two size classes (Figure 2). For logs, this relationship was initially negative and became positive with

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**Table 3** Summary of statistics from the serial model framework with richness of fungal fruiting species as response variable using linear mixed-effects models (LME). We show the standardized effect sizes of the parameter estimates using an expected mean of 0 (z values, estimates divided by the respective standard error); boldface indicates significant values. The marginal $R^2$ (variance explained by fixed factors) is given. Effects in parentheses were not significant in the basic model of the LME or the generalized linear mixed-effects model (GLME, Table S3) and were therefore not interpreted. The grey-shaded area represents the main treatment effects (without interaction). The first factor named is the reference factor.
succession (Figure 2). For branches, the relationship was consistently positive, and effect sizes were higher than for logs (Figure 2; Table 3, sample model). The number of species of beech and fir of logs and branches increased with the first 3 years and levelled off in the fourth year with one exception—the number of species on fir branches showed no clear trend across years (Figure 3).

Our mixed-effects models revealed host species, host size and year as important drivers of species richness (Table 3, Table S2). Beech harboured more species than fir, and logs harboured more species per surface area than branches (Table 3, Table S2). Local dead-wood amount and heterogeneity had no significant effect on species richness (Table 3, Table S2). Canopy openness showed no significant effect in the basic model of the GLME (Table 3, Table S2); therefore, we did not consider this effect as significant.

We found four significant interactions (Table 3, Table S2): between host species and year (the richness increase between 2012 and 2013/2014/2015 was stronger for beech than for fir), between canopy openness and year (the richness difference between 2012 and 2013/2014 was higher under shady canopies than in sunny gaps), between host species and canopy openness (the richness difference between beech and fir was lower under shady canopies than in sunny gaps), and between canopy openness and host size (the richness difference between logs and branches was lower under shady canopies than in sunny gaps).

### 3.2 Community composition

The community composition was mainly driven by host species (Figure 4, Table 4, Table S3). Moreover, canopy openness, host size

![Figure 1](image1.png)

**Figure 1** Variance partitioning of the number of fruiting species of fungi and community composition of fruiting species between two variables sets. The variance was partitioned between the host set (host species and size) and the environmental set (stand microclimate and local dead wood). The explained variance was 61.6% for fruiting species richness and 9.2% for community composition of fruiting species. Remaining variance was attributed to the year, which was included as covariate.

![Figure 2](image2.png)

**Figure 2** Scatterplots of number of fruiting species of fungi in relation to surface sampled by year and size. Note the log-scale of the x- and y-axes. The y-axis for logs is displayed at the top; the y-axis for branches is displayed at the bottom. Shown are raw data for single objects and the line of best fit with the predicted confidence interval.
FIGURE 3  Box plots showing number of fruiting species of fungi by years (2012–2015), separate for host species (fir, Abies alba; beech, Fagus sylvatica) and size classes. Note the log-scale of the y-axis. Black dots indicate the medians; boxes indicate the lower and upper quartiles; grey dots are outliers; and error bars are the minimum and maximum without outliers. Angiosperm tree image by Michele M. Tobias (see Acknowledgements) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4  Ordination of the community composition of fungal fruiting species based on constrained correspondence analysis (CCA). Abundance data were square-root transformed. We used year, canopy openness, size, local dead-wood amount and local dead-wood heterogeneity as constraint environmental variables. Displayed are the two main drivers of the community composition, namely host species and canopy openness. Size had a minor effect (see Table 2). Note that most of our environmental variables are factorial treatments, which cannot be easily displayed as arrows within the CCA. Angiosperm tree image by Michele M. Tobias (see Acknowledgements) [Colour figure can be viewed at wileyonlinelibrary.com]
and year also showed significant relationships with the community composition (Figure 4, Table 4, Table S3). We found no significant overall effects of local amount and heterogeneity of dead wood on the community composition (Table 4, Table S3; note that we considered an effect as significant only if the effect was significant in both the ANOVA-CCA and the LME-CA model).

We found four significant interactions (Table 4, Table S3): between host species and year (the difference in the community composition between beech and fir increased with time) and between canopy openness and year (the difference in community composition between 2012 and 2013/2014/2015 was higher under shady canopies than in sunny gaps), between host species and canopy openness (the difference in community composition between beech and fir was higher under shady canopies than in sunny gaps), and between host species and host size (the difference in community composition between beech and fir was higher on branches than on logs).

4 | DISCUSSION

In this study, we quantified the effects of the host (tree species and size) and the environment (stand microclimate: sunny gaps and shady canopies, local dead wood: amount and heterogeneity of dead wood) on the community composition of fruiting species of fungi. The serial model was fit using ANOVA-like permutation tests based on constrained correspondence analysis (CCA). Boldface indicates highly significant values ($\chi^2 > 0.15$). The adjusted $R^2$ of the CCA is given. The grey-shaded area represents the main treatment effects (without interactions).

### TABLE 4

Summary of statistics from the serial model framework using community composition of fruiting species of fungi as response variable. The serial model was fit using ANOVA-like permutation tests based on constrained correspondence analysis (CCA). Boldface indicates highly significant values ($\chi^2 > 0.15$). The adjusted $R^2$ of the CCA is given. The grey-shaded area represents the main treatment effects (without interactions).

|                         | ANOVA-CCA | Basic | Final |
|-------------------------|-----------|-------|-------|
|                         | Sample    | Basic | Final |       |
| **χ²**                  | F         | Pr(>F)| F     | Pr(>F)|       |
| Year                    | 0.49      | 15.58 | 0.001 | 0.49  | 17.50  | 0.001 |
| Host size               | 0.20      | 18.79 | 0.001 | 0.20  | 21.10  | 0.001 |
| Host species            | 0.71      | 71.89 | 0.001 | 0.71  | 76.04  | 0.001 |
| Canopy openness         | 0.29      | 28.75 | 0.001 | 0.29  | 30.44  | 0.001 |
| Local amount of dead wood | 0.02     | 1.70  | 0.002 | 0.02  | 1.78   | 0.002 |
| Local heterogeneity of dead wood | 0.03 | 1.32  | 0.008 | 0.03  | 1.39   | 0.007 |
| **Year: Host species**  | 0.32      | 11.36 | 0.001 |       |       |       |
| **Year: Canopy openness** | 0.13   | 4.79  | 0.001 |       |       |       |
| **Year: Host size**     | 0.13      | 4.74  | 0.001 |       |       |       |
| **Year: Local amount**  | 0.02      | 0.86  | 0.967 |       |       |       |
| **Host species: Canopy openness** | 0.19 | 20.33 | 0.001 |       |       |       |
| **Host species: Local heterogeneity** | 0.03 | 1.51  | 0.001 |       |       |       |
| **Host species: Local amount** | 0.02 | 2.44  | 0.001 |       |       |       |
| **Host size: Host species** | 0.22 | 23.01 | 0.001 |       |       |       |
| **Host size: Canopy openness** | 0.05  | 5.76  | 0.001 |       |       |       |
| **Host size: Local heterogeneity** | 0.03 | 1.34  | 0.004 |       |       |       |
| **Host size: Local amount** | 0.01  | 1.55  | 0.006 |       |       |       |
| **Canopy openness: Local amount** | 0.01 | 1.18  | 0.134 |       |       |       |
| **Local amount: Local heterogeneity** | 0.03 | 1.39  | 0.002 |       |       |       |
| **Year: Host size: Sampled surface** | 0.24 | 2.81  | 0.001 |       |       |       |
| Residual                | 16.77     | 15.74 |       | 14.66 |       |       |
| Adj. $R^2$              | .04       | .10   |       | .15   |       |       |
wood added to a plot) on the fungal richness and community composition on single dead-wood objects over time. Our analysis was based on an orthogonal experiment that allowed identification and quantification of independent effects of these variables, which are usually correlated in observational surveys. Variance partitioning revealed that the host was a more important driver of species richness and community composition than the environment. Among all individual treatment variables, we found that the host species had the highest relative effect on the diversity of wood-inhabiting fungi on a dead-wood object. Canopy openness significantly affected the community composition. The host size had significant but rather small effects on species richness and community composition. By contrast, local amount and heterogeneity of dead wood showed no significant effects on species richness and community composition.

### 4.1 The importance of host species and size

Among the investigated variables, host species was important throughout all models of species richness and explained most of the variation in the community composition (Table 3, Table S2). Specialization of wood-inhabiting fungi on species of a particular host genus and to a lesser extent on a tree species have been documented (Baber et al., 2016; Heilmann-Clausen & Christensen, 2005; Heilmann-Clausen et al., 2016). Especially wood of gymnosperms and angiosperms differ in numerous properties (Cornwell et al., 2009; Kahl et al., 2017), and many wood-decaying fungi show preferences for one of these two major plant lineages (Gilbertson, 1980; Hibbett & Donoghue, 2001; Hoppe et al., 2015). Such clear differences in preference for gymnosperm and angiosperm trees have also been shown for assemblages of phytophagous insects (Brändle & Brandl, 2006). Furthermore, our results showed that the effect of year differed between host tree species, as indicated by their interaction (Table 3). This result points to clear differences between the two host species in their successional trajectories. However, we did not measure decomposition explicitly, and the decomposition process can succeed at very different rates in different tree species (Weedon et al., 2009); thus, we did not interpret this interaction as a difference in decomposition between tree species.

We are far from having a complete mechanistic understanding of why fungal communities differ between host species and why the communities show different successional trajectories. The differences in fungal communities between beech and fir might be due to both abiotic and biotic factors (filters) and their interactions. It is well known that species of host trees differ considerably in their physicochemical properties and hence in basic habitat conditions for fungi (Cornwell et al., 2009; Hoppe et al., 2015; Kahl et al., 2017). However, recent studies have also shown the importance of endophytic fungi of wood, which are prevalent even in living trees and are able to switch to a saprophytic lifestyle after the death of the tree (Parfitt, Hunt, Dockrell, Rogers, & Boddy, 2010; Promputtha et al., 2007; Song et al., 2017). Activity of this primary colonizer community also potentially influences micro-habitat conditions of the host tree via modification of woody compounds (e.g. lignin, cellulose decay with cell wall density loss; Schilling, Kaffengerber, Liew, & Song, 2015; Song et al., 2017) and related metabolites plus the possible response (production of secondary metabolites) of the host (Hiscox et al., 2015). The endophytic community is most likely primarily driven by the identity of the host species, that is, angiosperm vs. gymnosperm, and secondarily by the vitality of the host (Schwarze, Engels, & Mattheck, 2000), which could also contribute in explaining differences in diversity patterns between hosts (Figure 4, Table 4). However, to the best of our knowledge, no study has demonstrated the differences in wood-endophyte communities of angiosperm and gymnosperm trees. Although we did not determine the endophytic community at the beginning of the experiment, we detected fruit bodies of 5 of 11 known endophytic species on beech objects (angiosperm wood) (Biscognauxia nummularia, Eutypa spinosa, Fomes fomentarius, H. fragiforme and Stereum rugosum; Figure S5). Most species were missing in the fruit body record in the first year after exposure; however, the five detected species were found after 4 years. Interestingly, H. fragiforme was highly abundant at the start and across all years, and was the most abundant species in our experiment (Table S1, Figure S4). This observation supports the view that species known as endophytes are prevalent after tree death in consecutive years. Experiments have demonstrated that the identity and abundance of primary colonizers can have effects on species communities of later decay stages (known as “priority effect”), which can differ with tree species (Hiscox, Savoury, et al., 2016; Hiscox et al., 2015; Leopold et al., 2017). More studies are needed to disentangle the complex interactions between abiotic and biotic effects driving the differences in fungal communities among host species.

Our model framework, which standardized for the sampling effort, revealed a significant negative difference between branches and logs. This means that logs harbour on average a higher number of species per surface area of an object than branches. One possible explanation for the observed pattern might include the more cryptic variation in dead-wood characteristics within a log compared to a branch. For example, temperature, wood density, water content and decay stage can considerably vary within large logs (e.g. Graham, 1924; Leather, Baumgart, Evans, & Quicke, 2014; Saint-Germain, Buddle, & Drapeau, 2010). Therefore, the effect of dead-wood size might include an increase in the number of habitats (niches), that is, habitat heterogeneity, which is an important driver of saproxylic beetle richness (Seibold, Bässler, Brandl, et al., 2016).

### 4.2 The importance of the stand microclimate

Our models consistently revealed a significant effect of microclimate on the community composition. This effect indicates that fungal species differ in their preferences for microclimate conditions and suggests that wood-inhabiting fungi are adapted to different microclimates. Norros, Karhu, Nordén, Vähätalo, and Ovaskainen (2015) showed that sunlight and freezing causes severe spore mortality,
which supports the view that microclimate is an important environmental filter for wood-inhabiting fungi. Moreover, in our models, we found a significant interaction of host species and canopy openness (Table 4, Table S3). Based on a visual inspection of the ordination (Figure 4, Figure S6 for unconstrained CA), this interaction suggests that the community composition of beech and fir is more similar in sunny gaps than under shady canopies (Table S3). Beech and fir specialists seem to form more distinct communities under shady canopies, which are characterized, for example, by microclimatic conditions with fewer and lower temperature amplitudes than in sunny gaps. Sunny gaps are characterized by a harsh microclimate (e.g. more temperature extremes), which might be unfavourable for host specialists, and thus opportunistic species become predominant and communities become more similar. An example of a host specialist is *Amylostereum chailletii*. This species was recorded only on fir and occurred on 84% of all occupied objects under shady canopies and on only 16% of the objects in sunny gaps. An example of a host opportunistic species that becomes more abundant in sunny gaps is *Coniochaeta pulveracea*. This species was recorded on both beech (74%) and fir (26%) but occurred on 96% of all occupied objects in sunny gaps. Species of the genus *Coniochaeta* consist mainly of very small, black, hard fruit bodies, and it is known that some even survive fires, which are adaptations that suggest that *Coniochaeta* sp. are specialists of harsh microclimate conditions (Wicklow, 1975). However, at present, we have only a limited understanding of the morphological and physiological adaptations of fungi to environmental conditions (Norros et al., 2015; Pringle, Vellinga, & Peay, 2015) and how they relate to different host species and subsequently influence assembly processes.

Species richness, in contrast to the community composition, was not significantly affected by canopy openness (Table 3). Some of the few existing studies have suggested that canopy openness reduces the number of species (Bässler, Müller, et al., 2010; Horák et al., 2016) and another reported no effect (Bässler et al., 2016). One explanation for the conflicting results might be that these studies were based on survey data, in which important drivers of species richness were either unknown or correlated, which leads to confounding effects. In survey studies, the history of the dead-wood objects is usually unknown. The cause of death, however, can have strong effects on the species diversity, which might overlay effects of microclimate (Boddy, 2001; Nordén et al., 2004; Renvall, 1995). For example, mortality might be caused by large-scale windthrow or insect-pest disturbance, in contrast to thinning under a dense canopy with patchily distributed dead wood throughout the year (Fricker, Bebber, & Boddy, 2007). Thus, different levels of canopy openness (and thus microclimates) are created depending on the cause of death. Furthermore, the way a tree dies affects the chemical and physical properties of the log or branch (Stokland et al., 2012), and consequently, this affects how the subsequent decay succession proceeds (Ottosson, 2013; Renvall, 1995; Stokland et al., 2012). In addition, the amount of dead wood in survey studies is often correlated with microclimate; larger gaps, for example, caused by a disturbance event, are not only correlated with more dead wood, but also alter the stand microclimate. In such a scenario, it is furthermore not possible to disentangle effects of dead-wood amount and dead-wood heterogeneity (see above and Bässler et al., 2016; Müller & Büttler, 2010; Seibold et al., 2015). Our study overcame such confounding effects by standardizing the history of the hosts (trees of the same history and age harvested from one stand), cause of death (cutting by chainsaw), local dead-wood amount, local dead-wood heterogeneity and one of two microclimate conditions (either sunny gaps or shady canopies). Hence, a similar number of species but a clear difference in the community composition supports the view that fungal species are adapted to different microclimates.

### 4.3 Effects of local amount and heterogeneity of dead wood

Against our expectation, the local amount and heterogeneity of dead wood on a plot had no significant effect on species richness on a single dead-wood object (Table 3, Table S2). Furthermore, we did not find a tendency for this pattern to change over time (no significant interaction terms). When the amount of dead wood on a plot is high, we expected that more individuals would be able to coexist in an area owing to the larger area (species pool). Clearly, spores can disperse over long distances (Brown & Hovmøller, 2002; Hallenberg & Küffer, 2001); however, the probability of colonization decreases with distance, and the majority of sources for successful colonization might be located some hundred metres from the considered object (Norros et al., 2012) or even less (Galante, Horton, & Swaney, 2011). Thus, we expected that local dead wood would increase the species richness of an object nearby. Some of earlier studies supported this view (Edman et al., 2004), other studies did not find an effect of local enrichment on the diversity of fungi on a dead-wood object in the surroundings (Olsson et al., 2011; Rolstad et al., 2004). Rolstad et al. (2004) suggested that there was no dispersal limitation at the scale of their study. Thus, spores and mycelia might be omnipresent at the scale of our study as well (landscape covering c. 24,000 ha), and wood-inhabiting fungi are not limited in their ability to colonize dead wood, at least in the early successional stage. Another explanation for the mechanism behind this pattern might be that the early colonization and subsequent species diversity determines the subsequent communities. As outlined above, it has been shown that numerous wood-decay fungi are latently present as endophytes in sapwood of a wide range of still-living angiosperm trees (Parfitt et al., 2010). The endophyte community might therefore act as a filter and determine the secondary colonizers and subsequent communities independent from local donors or the number of colonization events. Therefore, the lack of a significant effect of the local dead-wood amount might be caused by priority effects (Fukami et al., 2010; Hiscox et al., 2015). The priority effect states that the succession of species communities is affected by the predecessor community. However, we aimed at focusing on the very early stage of succession, with species from the endophytic and secondary colonizer communities (Boddy, 2001; Parfitt et al., 2010; see Table S1 for...
the local dead-wood amount and heterogeneity at the scale of our study are not important for species richness and community composition on single dead-wood objects in the early phases of wood decomposition. Further studies are needed to shed light on the distribution and relevant scale of donor populations affecting the colonization of a dead-wood object within and across landscapes and to untangle these processes from priority effects.

5 | CONCLUSIONS

Our study demonstrated that host is a more important driver of the diversity of fruiting species of fungi than the environment. A closer look revealed that the host species had the highest relative effect on the diversity of woody-inhabiting fungi, followed by microclimate and host size, but not local dead wood. We hypothesize that the combined effects of tree species and canopy openness leads to a preponderance of host specialists under shady canopies that shift towards communities dominated by host opportunists or microclimate harshness specialists in sunny gaps. For the conservation of wood-inhabiting fungi, forest managers should provide dead wood of a broad range of tree species, exposed to different microclimatic conditions. This goal can be achieved most efficiently by enriching dead wood of larger sizes during regular logging activities independent of the availability and distribution of existing dead wood in the surroundings.

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AUTHORS’ CONTRIBUTIONS

C.B., J.M., P.B. and R.B. designed the concept of the study; F.K. and C.B. analysed, interpreted and wrote the manuscript; R.B. contributed to data analysis; S.S. contributed to data collection and interpretation of the data. All authors critically revised the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.b3d97 (Krah et al. 2018).

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the supporting information tab for this article.

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