Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models

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ABSTRACT

We assessed how environmental drivers influence the occurrences of wood-inhabiting macrofungi in European beech forests, using an extensive dataset of fruit body records collected in 53 reserves across twelve European countries. We found that the 105 species included in this study varied greatly in their responses to covariates related to resource quality, climate and forest connectivity, both in the strength and direction of the observed effects. Climate was the most important driver for some species, while others responded more to connectivity, or simply to the presence of high quality substrates within the reserves. Species occurrences varied also across geographical regions, especially between the UK and the rest of Europe. Our results show that wood-inhabiting fungi in European beech forests respond individualistically to habitat filters and differ in their biogeographical distribution patterns, and they thus provide a detailed perspective of how wood-inhabiting fungal communities are structured across Europe.

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1. Introduction

Communities of wood-inhabiting fungi are filtered by local factors related to dead wood quality and by regional factors related to climate, landscape history and forest naturalness (Heilmann-Clausen and Boddy, 2008; Junninen and Komonen, 2011; Heilmann-Clausen et al., 2014; Abrego et al., 2015). A broad body of literature has shown that wood-decay stage, associated tree species and size of the dead wood unit are the most important factors influencing fungal community composition at the finest spatial scale (i.e. the dead wood unit) (e.g. Küffer et al., 2008; Yamashita et al., 2010; Stokland, 2012; Rajala et al., 2015). At the

landscape scale, macroclimatic factors and factors related to forest naturalness, such as management history and connectivity, are of greater importance (e.g. Penttilä et al., 2006; Halme et al., 2013; Nordén et al., 2013; Heilmann-Clausen et al., 2014; Abrego et al., 2015; Fukasawa and Matsuoka, 2015).

Nevertheless, much of the variation seen in the wood-inhabiting fungal community composition has remained unexplained in most studies (e.g. Abrego et al., 2014, 2015; Heilmann-Clausen et al., 2014; Juutilainen et al., 2014). This might be due to a combination of stochastic community assembly processes and a failure to identify the relevant environmental constraints. Wood-inhabiting fungal communities are composed of many species, which differ in their individual responses to the environment. For instance, species show very individualistic optima in relation to the successional process of wood decay (e.g. Rajala et al., 2015), as well as for the size and type of inhabited dead wood unit (e.g. Küffer et al.,

2008; Hottola et al., 2009). Likewise, although most wood-inhabiting fungal species respond negatively to forest management practices causing dead wood reduction and fragmentation (e.g. thinning and clear-cutting activities), human disturbance can be beneficial for some species (Müller et al., 2007; Nordén et al., 2013). Wood-inhabiting fungi can also respond differently to macroclimatic conditions, as some species are better adapted to continental climatic environments than others (Ódor et al., 2006; Bässler et al., 2010). In addition to showing interspecific variation in their responses to differing habitat conditions, wood-inhabiting fungi are subjected to other biogeographical forces such as historical speciation and extinction processes which also influence their current regional distribution. Thus far, the relative importance of these individual factors has mainly been studied at the community level, using species richness or community similarity as the response variable (e.g. Abrego et al., 2014; Heilmann-Clausen et al., 2014; Juutilainen et al., 2014; Fukasawa and Matsuoka, 2015). Thus, a species-specific assessment of the factors influencing the broad-scale distribution patterns of all species forming wood-inhabiting fungal communities can provide a more detailed insight into the spatial structure of these communities.

European beech (*Fagus sylvatica*) is a widespread tree species in Europe and constitutes one of the principal natural vegetation types on the continent (Pott, 2000; Brunet et al., 2010). Its distribution ranges from the mountains in the Mediterranean region in the South, to Southern Scandinavia in the North, and from the temperate region and mountains in the Iberian Peninsula in the West to the eastern foothills of the Carpathians and Crimean Peninsula in the East. Beech has been present in Europe since the early Holocene, and has since been subjected to several glaciations resulting in repeated retractions and expansions. It has reached its current distribution range by non-simultaneous expansions originating from several glacial refugia (Magri et al., 2006; Magri, 2008). The most recent major colonization event of beech in Europe was in the British Isles, where it arrived ca. 2000–3000 years BCE (Magri et al., 2006; Magri, 2008). Its distribution limits can be explained mainly by its sensitivity to dry summers and extremely cold winters (Fang and Lechowicz, 2006). As is the case for many other organisms, the North Atlantic Oscillation is an important factor delimiting the distribution of European beech, as it strongly influences the temperature and amount of precipitation in Europe (Ottersen et al., 2001).

The distribution range of European beech offers a suitable area for studying large scale distributions of wood-inhabiting species, not only because of the broad geographic range itself, but also because of the macroclimatic variation and differing degrees of habitat fragmentation across this area (Metzger et al., 2005; Parviainen, 2005; Heilmann-Clausen et al., 2014; Abrego et al., 2015). Climatically, although European beech is confined to the temperate zone, it experiences a Mediterranean influence towards its southern distribution limit, and an increasing continentality gradient towards the East (Metzger et al., 2005). The long history of land use in Europe has led to a highly fragmented beech forest landscape, especially in its northern and western distribution areas (Parviainen, 2005; Kaplan et al., 2009).

In this study, we analysed the species-specific responses of wood-inhabiting fungi to the main drivers known to explain community gradients in such organisms, using an extensive dataset collected in a standardized way in beech forest reserves across twelve European countries (Austria, Belgium, Bulgaria, Denmark, England, Germany, Hungary, Italy, the Netherlands, Slovakia, Slovenia, Sweden and the UK). The main objective was to explore the interspecific variation in species' responses to environmental factors, in order to get a more comprehensive understanding of their broad-scale distribution patterns. More specifically, we aimed

to: (1) measure the relative importance of connectivity, macroclimate, resource quality and regional effects in explaining the fruiting occurrences of wood-inhabiting fungal species within European reserves; (2) illustrate species-specific variation in the responses of wood-inhabiting fungi to the same covariates; (3) assess the factors influencing the distribution patterns of the indicator species proposed by Christensen et al. (2004).

2. Materials and methods

2.1. Study area and field data inventories

The dataset used in the present study was compiled from the 41 European beech forest reserves used in Abrego et al. (2015) and 12 additional reserves from three additional countries (see Supplementary Appendices 1 and 2 for the names and locations of sampled reserves). The criteria for site selection and survey design were the same as described in Abrego et al. (2015). Briefly, the main criteria for site selection were that sites should represent, as far as possible, the best examples of natural beech forests within each country and that, taken together, their locations should represent the distribution of European beech.

Fungal sampling was carried out between 2001 and 2014, during the main fruiting season in each European region (from late August to early November), surveying each dead wood unit (fallen beech trunks of at least 10 cm in diameter including their standing snag if present) one to three times. In each reserve, we attempted to cover all decay classes following the 1–5 classification system devised by Christensen et al. (2005), and to survey equal numbers of dead wood units per decay class. At the dead wood unit level, the fruiting presence of the following selected wood-inhabiting macrofungal species was recorded: polypores, agarics, pileate corticioids, thick resupinate corticioids (species from the genera, *Dentipellis, Phlebia, Steccherinum* and *Xylobolus*), larger discomycetes and stromatic pyrenomycetes. Most species were identified in the field, but when microscopic identification was necessary, specimens were collected and dried for further study in the laboratory.

2.2. Measured covariates

Our selection of environmental variables was based on those shown to significantly influence wood-inhabiting fungal species communities, based on results of our previous studies analyzing partly the same data (Ódor et al., 2006; Halme et al., 2013; Heilmann-Clausen et al., 2014; Abrego et al., 2015). The environmental variables included in this study are described in Table 1 and detailed in Supplementary Appendix 2. At the dead wood unit level, diameter at breast height and decay stage were recorded in the field. At the reserve level, annual precipitation, mean annual temperature, annual temperature range, connectivity at the 10 km spatial scale, area of the reserve and number of surveyed dead wood units were recorded. For characterizing respectively the mean annual temperature, annual temperature range and precipitation in the reserves, we used the climatic GIS layers BIO1, BIO 7 and BIO12 of Hijmans et al. (2005). Connectivity at the 10 km scale was computed for each reserve following the same procedure as described in Abrego et al. (2015), using Zonation Conservation Planning Software (Lehtomäki and Moilanen, 2013) and maps produced by Brus et al. (2012). To control for the effect of the sampling effort, we also included the number of sampled dead wood units as a reserve level covariate. The reserves were grouped in eight regional categories (henceforth called regions), according to their geographical location (see Supplementary Appendices 1 and 2).

Table 1
Description of the variables measured in the study. Their sources and measurement procedures are explained in the Methods section.

Group of variables	Name	Description	Variable type, units and transformation
Variables related to resource quality	Diameter	Diameter at breast height of the dead wood units surveyed in each reserve.	Continuous (log transformed), cm
	Decay stage	Decay stage of the dead wood units surveyed in each reserve.	Continuous, index from 1 to 5
Variables related to climate	Precipitation	Annual precipitation in the reserves.	Continuous, mm
	Mean annual temperature	Mean annual temperature in the reserves	Continuous, °C
	Annual temperature range	Annual temperature range in the reserves	Continuous, °C
Variables related to connectivity	10 km connectivity	Connectivity of the reserves to the neighbouring beech forests.	Continuous (log transformed), numerical index
	Reserve area	Area of the reserves.	Continuous (log transformed), ha
Variables related to the survey effort	Survey effort	Number of dead wood units surveyed in each reserve.	Continuous (log transformed)

2.3. Statistical analyses

All statistical analyses were carried out using the program R version 3.2.2 (R Development Core Team, 2015). We modelled the presence/absence at the time of survey of each fungal species both at the level of the dead wood units and the reserves, using logistic regressions with the function *lmer* from the lme4 package (Bates et al., 2015). In the analyses at the dead wood unit level we included dead wood unit and reserve level covariates as explanatory variables, with reserves nested within regions as a random effect. In the analyses at the reserve level we only included reserve level covariates, hence for the resource quality variables — diameter and decay stage — we averaged the values measured at dead wood unit level over the number of dead wood units that were surveyed in each reserve. In the latter models, we included regions as a random effect. All continuous explanatory variables were normalized to mean zero and standard deviation one. Additionally, as the responses of the species to the dead wood diameter and decay stage are often not linear but have a Gaussian distribution (i.e. the fruiting occurrences of wood-inhabiting fungal species peak at a given decay stage or diameter instead of increasing in a monotonic way), we included as explanatory variables the quadratic terms of the diameter values and decay classes. As an excess of zeros or ones in the response variables led to impossible model fits, for the dead wood unit level analyses we selected those species that fruited on at least 15% of the dead wood units in the study (there were no species which occurred on most dead wood units). Likewise, for the reserve level analyses, we selected those species that occurred in 20–85% of the reserves. To model those species which could not be included in the species-specific regression models, we additionally modelled as different groups the presences/absences of all very rare (those with one or two occurrences in the data) and rare (those with three or more occurrences but occurring in less than 20% of the reserves or 15% of the dead wood units) species, by using the same model structures as described above.

We assessed the total amount of variation explained by the logistic regression models by their Tjur R^2 values (Tjur, 2009). We then computed the proportion of the explained variation that was due to the random and fixed effects in the models. Likewise, we calculated how much of the variation explained by the fixed effects was due to the variables related to the resource quality, climatic-related variables, connectivity-related variables and sampling effort (the variables corresponding to each of these groups are described in Table 1). The proportion of the explained variation by each group of variables was computed following the equation $Var_{ij} = \sum_i \sum_j \beta_i \beta_j C_{ij}$, where i and j are the environmental covariates belonging to a given group, β the regression coefficients and C the variance-covariance matrix of the design matrix. Note that

following this formula, we accounted for the shared co-variation among variables within the groups, whereas we ignored the amount of co-variation among variables between the groups.

3. Results

Altogether, the full dataset consisted of 19,343 records of 341 fungal species on 1908 dead wood units (Supplementary Appendix 3). On average, every species occurred in 3% of the dead wood units and 22% of the reserves. Most species in the dataset were rare in the sense that they occurred in less than 20% of the reserves (Fig. 1A). Moreover, one third of the species were found only once or twice (Fig. 1B). Conversely, only 13 species were found in more than 85% of the reserves, but none of those were found on more than half of the dead wood units (Fig. 1).

Logistic regression models at the dead wood unit level were run for 20 species (those that occurred in at least 15% of the dead wood units), and for 17 of these, the models explained more than 25% of the variation in occurrence (measured by the Tjur R^2) (Supplementary Appendix 4). In these models, most species were influenced by the group of variables related to resource quality, followed by the reserve ID random effects (Supplementary Appendix 4 and Fig. S1 in Supplementary Appendix 5). Likewise, the groups of rare and very rare species were mostly influenced by resource quality when modelling their occurrences at the dead wood unit level (Supplementary Appendix 4).

At the reserve level, we ran logistic regression models for 105 species (common and semi-common species in Fig. 1A). For 92 species (27% of all species in the dataset) at least 25% of the variation in the occurrence patterns across the European reserves was explained by the included variables (measured by the Tjur R^2) (Supplementary Appendix 6). The species strongly varied in their response to the defined variable groups. Most species were influenced principally (in terms of variable groups explaining $\geq$50% of the Tjur's R^2) by a combination of climatic, connectivity, resource quality and region-related variables (36 species) or by the resource quality variables (20 species) (Fig. 2). Fewer species were primarily influenced by climate-related variables (13 species), connectivity-related variables (12 species) and regional effects (10 species). Only one semi-common species was primarily influenced by sampling effort, in addition to all very rare species (Supplementary Appendix 6). Rare species were mostly influenced by connectivity, followed by climate-related variables (Supplementary Appendix 6). In most cases, when a variable group explained $\geq$50% of the variation, at least one of the variables included in this group significantly influenced the occurrences of the species ($p < 0.05$) (Supplementary Appendices 4 and 6). As can be seen from the signs of the parameter estimates in Supplementary
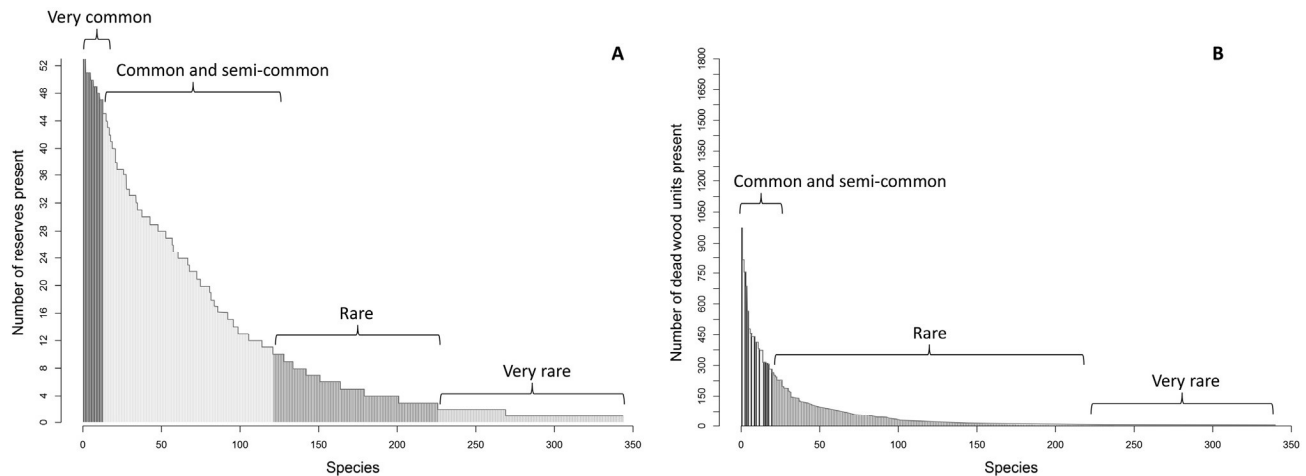
Fig. 1. Ranked occurrence distribution patterns of the species across the visited reserves (A) and sampled dead wood units (B). Different colours indicate the commonness of the species: very common (species found in 85% or more reserves, respectively of the dead wood units), semi-common (species found in 85%—20% of the reserves, or 85%—15% of the dead wood units), rare (species found in three or more reserves but less than 20% of all reserves, respectively less than 15% of all dead wood units), and very rare species (species found in one or two reserves, respectively dead wood units). Those species found in 85% or more reserves are indicated with black colour in (B). The full fungal names and respective numbers of occurrences are given in Supplementary Appendix 3.
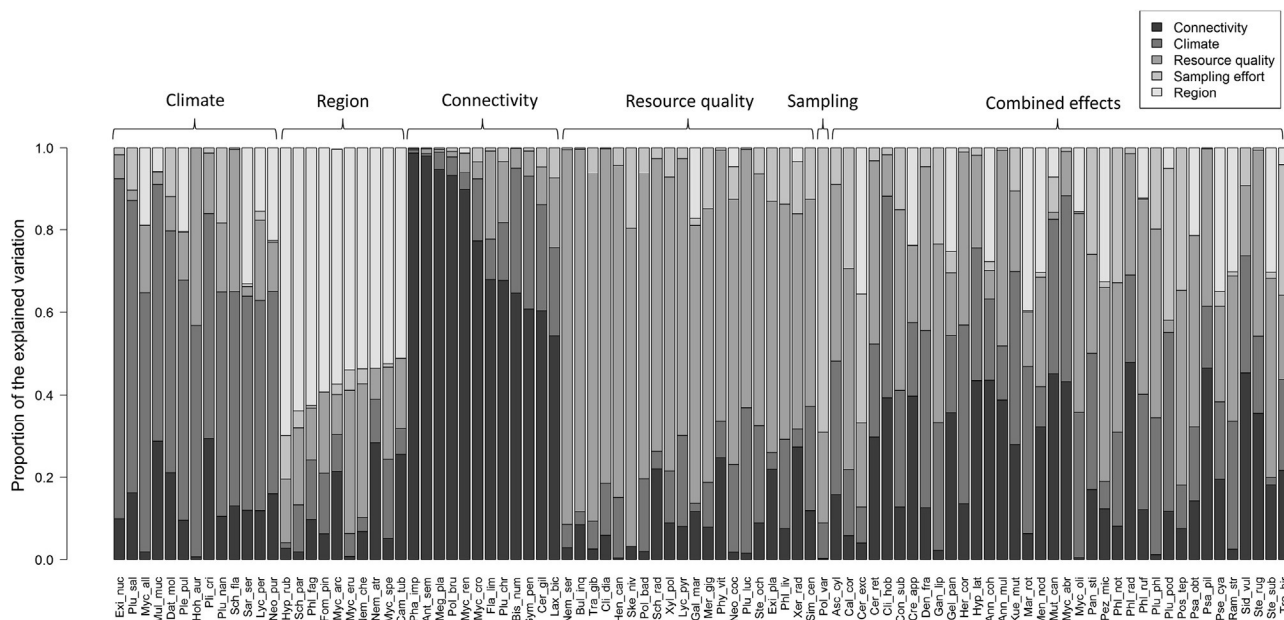
Fig. 2. Classification of the recorded fungal species in relation to the principal groups of variables that explain their occurrences across the sampled European reserves. The lengths of the coloured bars represent the fraction of the explained variation belonging to each group of variables: variables related to connectivity, climate, resource quality and regional effects (i.e. variation explained by the random effects in the models). Named groups of variables are shown where species occurrence was explained by at least 50% of the Tjur's R^2 values and 'combined effects' indicates those occurrences which were not dominantly explained by one group of variables. The full fungal names are given in Supplementary Appendix 6.

Appendices 4 and 6, the direction of the responses to the investigated environmental variables differed among fungal species.

As mentioned above, geographical regions captured most of the explained variation in occurrence for ten species (Fig. 2). Four of these species were stromatic pyrenomycetes (*Camarops tubulina, Hypoxylon rubiginosum, Nemania atropurpurea, Nemania chestersii*), and three *Mycena* species (*Mycena arcangeliana, Mycena erubescens, Mycena speirea*). The UK was the geographic region with the strongest regional effect on the distributions of wood-inhabiting fungi (Supplementary Appendix 5, Fig. S2), and hence we compared the different frequencies among the most common fungal species present in UK and the rest of Europe (Supplementary

Appendix 7). We found the strongest frequency differences in *Mycetinis alliaceus* (0% of dead wood units in UK and 26% in the rest of Europe), *Fomes fomentarius* (1%, 48%), *Ganoderma lipsiense* (= *applanatum*) (0%, 25%), *Fomitopsis pinicola* (0%, 10%) and *Ganoderma adspersum* (40% and 0%).

No indicator species occurred on more than 15% of the dead wood units, and so these were excluded from logistic regression models at the dead wood unit level. Similarly, in many cases the models failed to converge in the reserve level analyses due to the few occurrences of indicator species (this was the case for 9 out of 18 species) or the models explained less than 25% of the total variation (this was the case for *Pluteus umbrosus*). The eight

indicator species for which the models successfully explained at least 25% of the variation were as follows: *C. tubulina, Ceriporiopsis gilvescens, Dentipellis fragilis, Flammulaster limulatus, Gelatoporia pannocincta, Hericium coralloides, Hohenbuehelia auriscalpium* and *Phlebia nothofagi.* For these eight species, connectivity and reserve size generally positively influenced their occurrences (Table 2). For *C. gilvescens, F. limulatus* and *G. pannocincta*, connectivity was the main factor influencing their occurrences, as both area of the reserves as well as connectivity at the 10 km spatial scale (Table 2 and Supplementary Appendix 6). For *C. tubulina*, the geographic regions explained most of the variation in their occurrences across the European reserves, followed by connectivity-related variables. For *D. fragilis, H. coralloides* and *H. auriscalpium* climatic-related variables explained most of the variation, followed by the quality of the resources (Fig. 2 and Supplementary Appendix 6). For *P. nothofagi* the resource quality was the major determinant, followed by the sampling effort (Fig. 2).

4. Discussion

In this study we show that wood-inhabiting fungal species in European beech forests exhibit a range of responses to resource quality, climate and connectivity. The species-specific responses to environmental drivers were highly variable, both in the strength and direction of the observed effects. Additionally, the relative importance of different variable groups differed markedly among species. This shows that environmental filtering (*sensu* Kraft et al., 2015) plays an important but complex role in the large-scale assembly processes of wood-inhabiting fungal communities, through species-specific responses that are not easily distinguishable by traditional analyses of community similarity.

It is well known that resource quality is a very important habitat filter affecting the occurrence of individual species within and across sites (Küffer et al., 2008; Yamashita et al., 2010; Stokland, 2012; Rajala et al., 2015). However, climate- and connectivity-related variables were the main, but highly entangled, factors influencing community gradients in several continental-scale studies (Ódor et al., 2006; Heilmann-Clausen et al., 2014; Abrego et al., 2015; Fukasawa and Matsuoka, 2015). Here we disentangle the relative importance of these drivers, and show that climate is indeed the most important driver for some species, while others respond more to connectivity-related variables, or simply to the presence of high quality substrates within reserves. For many other species, there was not one principal habitat factor influencing their occurrences, but several different habitat factors (resource quality, climate and connectivity) contributed equally to explain their occurrence patterns. This highlights the multi-dimensional complexity of the relationship between habitat factors and fungal distributions.

Apart from fixed effects, random factors explained a large part of the variation in the occurrences of many species, especially at the smallest scales, i.e. at the level of dead wood units. With increasing spatial scale (i.e. from dead wood units to reserves), the amount of random variation captured by the models decreased, while the amount of variation explained by the measured covariates increased. This is in concordance with previous studies that have shown wood-inhabiting fungal communities to be particularly variable at small spatial scales (Bässler et al., 2012; Kubartová et al., 2012; Abrego et al., 2014). The high random variation detected at the dead wood unit level suggests that processes not included in our models influence the occurrences of wood-inhabiting fungi at this scale. Such mechanisms might include randomness in dispersal and establishment (Norros et al., 2014; Peay and Bruns, 2014), responses to abiotic environmental variables not measured in the present study, as well as biotic interactions among the species (Ovaskainen et al., 2016). Another factor potentially creating random variation in our study is that most dead wood units were surveyed once, thus a number of species were likely to remain undetected (Halme and Kotiaho, 2012; Abrego et al., 2016). This might have increased the number of rare species (i.e. species with few occurrences) in our dataset. Nevertheless, as has been shown by both molecular (Kubartová et al., 2012) and fruit body based surveys (Abrego et al., 2016), a high proportion of rare species is an inherent characteristic of wood-inhabiting fungal communities. Finally, we note that some of the species included in the dataset are cryptic species complexes (e.g. *Antrodiella semisupina, Physisporinus vitreus, Pluteus plautus* and *Skeletocutis nivea),* for which a more accurate taxonomic resolution might provide better model inferences (see Seierstad et al., 2013; Runnel et al., 2014).

For some species, the geographical regions captured most of the explained variation, meaning that after accounting for variables related to climate, forest connectivity and resource quality, their presence was mainly confined to particular geographical areas. This suggests that unknown biogeographical filters affect the current distributions of some wood-inhabiting fungal species. These filters could be related to historical geographical barriers impeding species' range expansions, or reflect different regional traditions of land use, affecting fungal communities in dead wood. Based on analyses of a subset of the data used in this paper, Heilmann-Clausen et al. (2014) observed that wood-inhabiting fungal

Table 2

Model outputs for the fruiting occurrences of fungal indicator species in the sampled European beech forest reserves. Note that since the variables were normalized for the analyses, the estimate values are directly comparable among them, i.e. negative mean values indicate that the variables negatively affected the occurrences of the indicator species. The <0.05 *p*-values are indicated by asterisks (*). For further details of the model outputs, see Supplementary Appendix 6.

Variable	Estimate and p-values							
	Camarops tubulina	*Ceriporiopsis gilvescens*	*Dentipellis fragilis*	*Flammulaster limulatus*	*Gelatoporia pannocincta*	*Hericium coralloides*	*Hohenbuehelia auriscalpium*	*Phlebia nothofagi*
Diameter	10.79	−2.41	9.94	−5.65	−2.47	1.22	0.47	1.12
Diameter^2	−14.80	3.29	−12.24	6.34	3.54	−1.73	−0.32	−0.64
Decay stage	21.18	−1.30	−4.57	−0.13	3.61	3.46	5.24	2.23
Decay stage^2	−20.29	0.79	2.99	0.20	−4.58	−2.53	−5.44	−1.16
Area	−0.88	1.18	−0.35	2.26*	2.46	0.48	−0.03	0.51
Temperature range	2.74	−0.45	3.77*	−0.37	−0.78	1.15	0.76	0.76
Precipitation	2.02	0.99	−0.64	−0.93*	−1.11	−0.53	−1.09	−0.05
Mean temperature	0.46	1.71*	−1.35	−0.23	−1.72	0.17	0.13	0.71
Connectivity 10 km	7.54*	2.26*	2.36*	0.83	0.56	−0.68	0.14	0.11
Number of logs	−0.03	0.05	0.09	−0.02	0.07	0.01	0.00	−0.07

communities, compared to co-occurring bryophyte communities, were only weakly structured in regional species pools. However, in Heilmann-Clausen et al. (2014), there was an attempt to capture regional differences using unconstrained multivariate methods at the community level, whereas in the present paper we used a species-specific model-based approach. This allowed us to distinguish between species that show a direct response to included continuous environmental gradients at the continental scale and those for which we can only detect a response to the geographic regions. Nevertheless, these results should be cautiously interpreted, as it is possible that broad scale environmental variables that are important for explaining the occurrences of certain species within geographical regions have remained overlooked. Further, phenological effects may also influence this result, especially for those species with ephemeral fruit-bodies such as *Mycena* species that might have been present as mycelia at some locations but not fruiting at the time of sampling (Halme and Kotiaho, 2012; Abrego et al., 2016). However, several stromatic pyrenomycetes, characterized by tough and persistent fruit bodies and hence not liable to phenological undersampling, were also strongly influenced by the geographical regions. This result coincides with the distribution patterns of pyrenomycetes in Scandinavia, which is correlated with the vegetation zones (Mathiassen and Halvorsen, 2007). Interestingly, many pyrenomycetes establish as endophytes in living woody host tissues (Boddy and Heilmann-Clausen, 2008), and their distribution patterns may, therefore, reflect historical expansions of different host populations rather than current climate or forest connectivity.

The UK was the geographical region showing the strongest regional effects on the European distributions of wood-inhabiting fungi, supporting the hypothesis that geographical barriers are important for defining regional species pools. The most striking difference was between the contrasting patterns of dominant perennial polypores in the UK and the rest of Europe, especially since these are among the most important primary decayers of beech trunks (Heilmann-Clausen and Christensen, 2003). While *F. fomentarius, G. lipsiense* and *F. pinicola* were the most common perennial polypores on large dead beech wood in continental Europe, they were almost absent from the UK sampling sites. Conversely, *G. adspersum*, a very rare species in beech reserves in continental Europe, was the dominant perennial polypore fruiting on fallen beech trunks in the UK. An explanation for this difference might be the recent establishment of beech in the UK (Magri et al., 2006), and the relative isolation from mainland Europe, which might have given *G. adspersum* the opportunity to take over the niche as a dominant trunk rot fungus, before species having roughly the same ecological niche in continental Europe could establish large populations. In addition, the British Isles are characterized by having a more oceanic climate than most parts of continental Europe, with higher average temperatures than other regions in the same latitudes, low variation in annual temperature ranges (relatively warm winters and cool summers), and high precipitation (Packham et al., 2012). This may affect the outcome of competitive interactions of wood-decayers in favour of *G. adspersum*. Finally, British forests and parks have traditionally retained a relatively large number of old (often pollarded) trees, despite a strong industrial demand for wood (Green and Peterken, 1997; Kirby et al., 1998; Packham et al., 2012). This may also have been beneficial to *G. adspersum* which, unlike the dominant polypores in continental Europe, causes basal heart rot initiated in living trees (Schwarze and Ferner, 2003).

Based on results from other studies (Penttilä et al., 2006; Nordén et al., 2013; Abrego et al., 2015), we expected connectivity-related variables to strongly influence the distributions of wood-inhabiting indicator species proposed by Christensen et al. (2004). For the analysed indicator species, our results confirmed that connectivity-related variables positively influence their occurrences, and that for some of them (notably, *C. gilvescens, F. limulatus* and *G. pannocincta*), connectivity was the main factor influencing their occurrences across the European beech reserves. For the indicator species *C. tubulina*, connectivity was the strongest determinant factor explaining its occurrences, after the regional effects. For other indicator species (*D. fragilis, H. coralloides, H. auriscalpium* and *P. nothofagi*), factors related to climate or the quality of dead wood had largest effects on their occurrences, whereas connectivity had a positive but minor role. As showed previously (Ódor et al., 2006), climatic and naturalness gradients are highly correlated within the expansion of European beech forests, hence this result suggests that the latter indicator species are more dependent on continental climates rather than on old growth forest connectivity as proposed by Christensen et al. (2004), as long as suitable dead wood habitats are available. On the other hand, our analyses support the proposal of other species, especially *Pluteus chrysophaeus* and *Biscogniauxia nummularia*, as potential indicators for natural beech forests at the European level. The former was already suggested as an indicator for the Netherlands and Belgium by Walleyn and Veerkamp (2005). However, we note that, due to the low number of occurrences of indicator species in the dataset, the species-specific modelling approach did not perform properly for many of them. Therefore, a more rigorous approach, including a balanced data sampling with more low quality sites, would be needed to test the reliability of potential indicator species in a more consistent way (cf. Halme et al., in press.).

Our results show how the species-specific responses of wood-inhabiting fungi to resource quality, climate, connectivity and geographic regions influence their individual fruiting distributions in Europe. Nevertheless the species-specific models failed to converge for most species, mainly those being very sparsely represented in the dataset and for which further data is required. Therefore, although our approach provides new knowledge about the drivers influencing the distribution patterns of many fungal species, we still lack a more general overview that takes account of all the species forming wood-inhabiting fungal communities.

Acknowledgments

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funeco.2016.07.006.

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