Substrate affinities of wood decay fungi are foremost structured by wood properties not climate

Fredrik Rustøen [a], Klaus Høiland [a], Einar Heegaard [b], Lynne Boddy [c], Alan C. Gange [d], Håvard Kauserud [a], Carrie Andrew [a, e]

[a] Section for Genetics and Evolutionary Biology (EVOGENE), University of Oslo, Blindernveien 31, 0316, Oslo, Norway

[b] Forestry and Forest Resources, Norwegian Institute of Bioeconomy Research, Fanaflaten 4, N-5244, Fana, Norway

[c] School of Biosciences, Cardiff University, Museum Avenue, Cardiff CF10 3AX, United Kingdom

[d] Department of Biological Sciences Royal Holloway, University of London, Egham, Surrey TW20 0EX, United Kingdom

[e] Oberlin College & Conservatory, Biology Department, 119 Woodland Street, Oberlin, Ohio, US, 44074

Email contact: carrie.j.andrew@gmail.com

Abstract

Wood decomposing fungi differ in their substrate affinities, but to what extent factors like wood properties influence host specialization, compared to climate, is largely unknown. In this study, we analysed British field observations of 61 common wood decay species associated with 41 tree and shrub genera. While white rot fungi ranged from low- to high-substrate affinity, brown rot fungi were exclusively mid- to high- affinity. White rot fungi associated with dead fallen wood demonstrated the least substrate affinity. The composition of wood decomposer fungi was mostly structured by substrate properties, sorted between angiosperms and conifers. Any relationships with temporal and regional climate variability were of far less significance, but did predict community-based and substrate-usage host shifts, especially for fungi on fallen deadwood. Our results demonstrate that substrate shifts by wood-decay fungi will depend primarily upon their degree of affinity to, and the distribution of, related woody genera, followed less at regional levels by climate impacts.

Keywords: affinity, climate, decay, reproductive traits, specialization, substrate usage, wood

Introduction

Assemblage patterns of fungal species are strongly linked to climate across large spatial scales (Andrew et al. 2018a), impacting distributions and ranges (Davis & Shaw 2001; Kelly and Goulden 2008, Wollan et al. 2008, Diez et al. 2020). Simultaneously, rapid changes in atmospheric greenhouse gasses and aerosols have drastically modified the global climate, perhaps most clearly manifested in mean annual temperatures. A prominent warming can be observed even in the past half century, in direct correlation with increasing fossil fuel emissions (Pachauri et al. 2014). Driving ecosystem dynamics, overall climate change can influence the biology of fungi (e.g., reproduction and phenology; Boddy et al. 2014), with consequences for species interactions and substrate associations (Allen et al. 2010; Gange et al. 2011).

The timing of fruit body production is different to that of half a century ago for many species (Boddy et al. 2014; Andrew et al. 2018b), and the shifts are direct consequences of climate (Andrew et al. 2018c). For example, in southern England the average fruiting period of 315 fungal species has more than doubled from 33.2 ± 1.6 d to 74.8 ± 7.6 d in the timespan of 1950 to 2005 (Gange et al. 2007). Kauserud et al. (2008) likewise demonstrated a similar pattern in Norway, when investigating the phenology of 83 agaricoid species. By utilizing large fungarium datasets of records from 1940 to 2006, they detected a delay in fungal fruiting by 13.3 ± 1.2 d across all species. While it is unquestionable that climate change is a cause of fungal phenological shifts (Andrew et al. 2018c), less clear is how the degree of affinity of fungi to their substrates might interact with climate-based impacts (Boddy et al. 2014).

Observations, especially in Great Britain, have suggested that the substrate affinity of wood decay fungi can change with time and is related to climate (Renvall 1995; Gange et al. 2011; Boddy et al. 2014; Bien & Damm 2020), but this phenomenon has not yet been linked to the degree of host specificity. Early criticism highlighted the need for systematic study (Heilmann-Clausen & Læssøe 2012); when more rigorous analyses were implemented, the results of wood decay host shifts remained, as did the more ecologically relevant questions regarding the causes, outside of climate, for host shifts (Gange et al. 2012) . However, active debate remains among scientists regarding this subject, suggesting further research is needed. More recent studies have implicated the importance of substrate characteristics to the diversity and composition of wood decay fungi (Purahong et al. 2018a; 2018b). Taken together, this emphasises the need to understand fungal dynamics in relation to substrate affinity(-ies), and alongside the influence of temporal change and climate.

Wood-decomposing fungi are especially suitable for investigating relationships between substrate affinity and climate for multiple reasons: wood rot fungi include many species that form macroscopic fruit bodies (Schmidt 2006), and which are easy to identify, ensuring taxonomic credibility. Many species also fruit frequently over time, providing multitudes of observer recordings, by which sampling bias is negated. Other wood decay fruit bodies may fruit less frequently but are robust and long-lived, another reason they are easier to observe and, hence, to measure reliably and analyse across time. Very recently, Runnel et al. (2021) similarly advocated their usage in conservation biology. As wood-decomposing fungi fruit from the woody substrate they rot, co-recorded substrate metadata are more readily available for wood decay fungi than others, e.g., soil-borne fruit bodies.

Ecologically, the brown- and white rot decay systems make them important decomposers and nutrient-cyclers in forest ecosystems. For example, in Europe alone, at least 393 polypore species have been recorded, with 99 of them (25%) classified as causing brown rot (Ryvarden et al. 2014). Recent genome analyses have shown that wood decay mechanisms are more diverse than previously thought and that a categorical classification of decay types into white rot and brown rot must be refined (Riley et al. 2014; Floudas et al. 2015). However, quantitative physiological or genomic information about decay types is currently not available. Wood decay roles are dual, and thus ecologically important, as they can sometimes also live as endophytes or pathogens in standing trees (e.g., heart, stem and root rots) as well as in decaying fallen logs and branches and stumps (Song et al. 2016).

Dynamics of wood decay fungi indicate that priority effects (Ottosson et al. 2014; Hiscox et al. 2015; 2016; Leopold et al. 2017; Norberg et al. 2019) as well as competitive interactions (van der Wal et al. 2016; Hiscox et al. 2018) shape communities and successional change. Wood properties are also important, for example wood chemistry (Fukasawa 2021; Lunde et al. 2022), decay stage (Holec et al. 2020) and stem diameter (Brazee et al. 2012). Less clear at this point, however, is the degree that fungal affinity, i.e., specialization to specific substrate taxa, might influence and inter-relate to climate effects.

In this study, we questioned whether any temporal and climate-related trends may be responsible for the substrate affinities of British wood decomposer fungi, from individual species' affinities to overall compositional trends. We utilized multi-source wood decay fungal fruit body records, for the past four decades, from across the mainland parts of the United Kingdom (UK; England, Wales and Scotland). By focusing on the UK, we could follow-up on research gaps in earlier substrate affinity studies (i.e., Gange et al. 2011; 2012,

Boddy et al. 2014), and within the same temporal period that climate conditions have changed in the UK, i.e., largely overlapping with the Gange et al. (2011; 2012) studies. Given that the UK offered strict differences in climate between the more oceanic western side, in contrast to the more continental eastern area, in this way we focused on the effect of climate on decomposer fungi's host associations and traits.

The research was based on three objectives: (1) To establish the degree of substrate affinity for the most commonly and consistently recorded wood decay species, in relation to ecological characteristics of the fungal taxa as well as their substrate genera. Fungal species were delineated by their reproductive traits and decay characteristics. Substrates were characterised as wood from either angiosperms or conifers. (2) Investigate the effects of climate on fungal composition between substrates, over a 40-y temporal scale. In this case, we were interested in both compositional changes related to temporal shifts, as well as differences between the east-west climate regions of the UK. (3) Determine the extent, through modelling, that fungal characteristics influenced their substrate affinities, in relation to climate and temporal change.

Materials and Methods

Data filtering and processing

Fungal multi-source data (museum specimens, citizen science and scientific observations) were extracted from the Fungal Records Database of Britain and Ireland (FRDBI: www.fieldmycology.net, www.frdbi.info) for all recorded fruiting events in the mainland UK countries of England, Scotland and Wales. Accompanying annotations on the associated substrate genera, the exact locations, and the year of observation were required. Records were taxonomically filtered to saprotrophic and pathogenic taxa found on woody substrates

(including taxa in the Polyporales, Hymenochaetales, Russulales, Thelephorales and including stereoid fungi) – this removed common species such as *Fistulina hepatica*, a well-known specialist of oak (*Quercus*) and sweet chestnut (*Castanea sativa*) in Great Britain. Fungal species with less than 100 total observations were removed, as were substrate genera with less than 10 fruit body records associated with them. Limiting the taxonomic scope was suitable for the goals of the project, and simultaneously reduced potential sampling bias by retaining only those taxa that were readily identifiable and with distributional prevalence (Cao and Larsen 2001). Temporal limitation of 1970 to 2010 captured the latest trends in temperature increase (Pachauri et al. 2014) while ensuring sufficient record amounts for analyses. The final dataset contained 53,094 records of 61 fungal species and 41 associated woody substrate genera.

A variety of climate variables were investigated for potential trends, entirely and across two equal time periods (1970-1990 and 1991-2010). Data were obtained from the Met Office in 2016, and overlain with a Watsonian vice-county map (a geographical division of the British Isles for the purpose of scientific data collection). The geography of the UK contributed to a longitudinal climate gradient that we used to divide, as appropriate for analyses, the climate and fungal data into two (multivariate) and eight (regression) zones (Supplemental Figure 1). Temperature (minimum, maximum and mean), and precipitation (total) were investigated at both annual and seasonal (meteorological spring, summer, autumn, and winter) aggregations. Mean annual temperature between the years and regions ranged from 8.07 to 9.65 ^{O}C, while maximum annual temperatures ranged from 11.34 to 13.43 ^{O}C, and minimum annual temperatures from 4.77 to 5.75 ^{O}C. Annual rainfall ranged from 746.11 to 1501.95 mm.

157 Fungal traits were extracted from Breitenbach (1986) and Ryvarden et al. (2014) for a variety
158 of reproductive and ecological characteristics: the general rot type (white or brown); the
159 fruiting frequency (annual or perennial, the latter defined as lasting two or more years); the
160 substrate stage when fruiting typically occurred (lying deadwood substrate (a combination
161 dead logs, stumps, and branches), or standing substrate (which could be alive or dead)) and
162 the average spore volume. While we were aware that specimen-based trait data, capturing
163 intraspecific variation, would be preferential, unfortunately such data were not available.
164 Traits were filtered to reduce multi-collinearity, with Pearson correlation used for continuous
165 variables, eta for continuous and categorical variables, and Cramer's V (phi) for two
166 categorical variables. Only non-collinear traits were included in the analyses. Substrate genera
167 were categorised as either angiosperms or conifers.
168
169 Genetic distance data contained the ribosomal DNA (rDNA) large subunit (LSU) 28S
170 sequences from GenBank (accessed October 26th 2015) for the study species. Sequences were
171 available for 39 of the 61 fungal species. The LSU region was optimal to use in this study due
172 to its limited mutation rate, making it possible to align the sequences across varying
173 taxonomic orders in the Basidiomycota. One representative LSU sequence was selected for
174 each of the 39 taxa. The sequences were aligned and pairwise genetic distances among all
175 taxa were calculated using MEGA5 (Tamura et al. 2011).
176
177 *Substrate specialization and substrate preferences*
178 To visualize the ranges of associations for substrates and fungal species and the potential
179 substrate affinities of the fungal species, a heat-map (package gplots in R) was generated
180 using the proportion of observations that were recorded for a given fungal species (61) across
181 the different woody substrate genera (41). Hierarchical clustering sorted the fungal species

from substrate generalist to specific, generating a sequence of substrate affinity, and the woody substrate genera from commonly to more rarely hosting the fruiting fungi. Trait and taxonomy attributes were added to the axes, selecting those as found important in the statistical models (described below).

The 28S LSU genetic distance data were correlated with a Simpson index of variation in substrate distributions among the fungal species, calculated as the difference in the Simpson 1-D index values between the species, to understand if genetic similarity related to substrate usage. The degree that genetic distance and the substrate-diversity distances matched was estimated with a Pearson correlation across all interspecific comparisons. We investigated how linear transformations of one matrix matched the other matrix with Procrustes analyses (package vegan in R; Oksanen et al. 2016). A large residual difference of the matrices would indicate a poor match between the genetic and Simpson index differences. The Procrustes analyses results were further verified through a permutation test (999 permutations) with a null-hypothesis that the Simpson index was independently distributed among the fungal species. The diversity distance matrix was recalculated for each species from permuted values and compared to the original genetic distances. If the observed correlation and Procrustes match was high, the permuted absolute correlation was assumed lower, and the residuals of the Procrustes larger. From these results, the correlation in genetic similarity and substrate usage was determined.

Compositional changes by substrate, time, region and climate

Each woody substrate genus was considered to host a fungal assembly, measured by the association of the fungal species with that genus. From the data we implemented a post hoc experimental design with replications by region (eastern or western UK), decade (1970s,

1980s, 1990s, 2000s), and the associated climate (mean annual temperature and precipitation). Little difference in fungal species composition on substrate genera between regions or decades would suggest few spatiotemporal changes in substrate specificities, hence little substrate specificity based on the prevailing climatic conditions. Greater compositional differences would, on the other hand, suggest substrate specificity changes for fungi on certain substrate genera.

By investigating the composition of decay fungi associated with woody substrate genera, we were able to examine the potential of climate-related shifts of fungi on their substrates, and in relation to spatiotemporal variance. We utilized canonical-correlation analysis (CCA) combined with variance partitioning. The compositional variability was dissected by the extent the available variables explained it, either individually or when confounded (Borcard et al. 2011). Forward selection of the 23 original Met Office variables identified the four variables that were included in the final analyses (mean annual temperature, decadal time period, region, and substrate genus). Four decadal time periods (1970's, 1980's, 1990's, and 2000's) and two climate-driven regions (eastern and western UK; Supplemental Figure 1) were selected. To reduce any possible effects of different sampling efforts between regions, the data were transformed to presence-absence of fungal species per substrate, region and time period. Two substrate genera (*Euonymus* and *Ribes*) and the one fungal species that associated most often with them, *Phylloporia ribis*, were outliers and were subsequently removed from the analyses. The variance attributable to spatiotemporal effects was constrained in the CCA, so as to focus upon the dominating impacts of climate and substrate genera.

Influence of fungal traits and climate on substrate usage

A fourth-corner and RLQ analysis explained how fungal traits on a compositional level related to the fungal habitat, i.e., plot-level variables of environment and substrate (Dray et al. 2014). The variables as previously selected in the CCA and variance partitioning analyses were included. A correspondence analysis was run for the continuous variables. A Hill-Smith analysis was utilized on matrices with both categorical and continuous variables (Brown et al. 2014; Dray et al. 2014). Randomization procedures implemented 49,000 permutations and the *P* values were adjusted for multiple testing with the false discovery rate procedure (Dray et al. 2014). From these analyses, directional correlations were generated based on the trait trends in the fungal species composition by those of the habitat variables.

For temporal analyses related to trait characteristics between fungal species and the woody substrate genera, Bayesian inference applying Integrated Nested Laplace Approximation (INLA) was utilized (Rue et al. 2009). From the total fungal occurrences on substrates, we could assess whether there was a temporal change induced by the trait of a fungal species. The statistical specifications followed that outlined for trait-specific multivariate regressions (Jamil et al. 2012) and the community assembly by traits (Brown et al. 2014), using a negative binomial distribution. In this case, we investigated if there was an effect of traits on fungal occurrences between two equal time periods, 1970-1990 and 1991-2010. The shared effects among species of the same trait were analysed, while allowing individualistic species responses by time period, with paired substrates across the time periods. The analyses were conducted in R version 3.2.2 using the following packages: vegan, MASS (Ripley 2011), ade4 (Dray and DuFour 2007), and R-INLA (Rue et al. 2009).

Results

Substrate specializations

In our UK study sample, the decomposer fungi that demonstrated the greatest substrate specialisation (≥ 95% of occurrences with one substrate and any other genera ≤ 1%) were associated with birch (*Betula*) and oak (Figure 1; Supplemental Table 1). Those fungal species with greatest affinity for birch were *Fomitopsis betulina* (= *Piptoporus betulinus*) and *Inonotus obliquus*, although each were recorded on more substrates than birch, with 8 and 5 total tree genera, respectively. Those species mostly specializing with oak were *Piptoporus quercinus*, *Daedalea quercina*, and *Pseudoinonotus dryadeus*, which were recorded with 1, 12 and 9 total substrate genera, respectively.

Further species that were recorded on few substrate genera, but which demonstrated less specificity, were (Figure 1; Supplemental Table 1): *Hericium erinaceus* with 4 recorded substrate genera, but 92% of occurrences with beech (*Fagus*); *Hericium cirrhatum* with 7 recorded substrate genera, but 83% of occurrences with beech; and *Coriolopsis gallica* which was associated with 5 recorded substrate genera, although 50% of occurrences were with beech and 39% with ash (*Fraxinus*). The species with overall less substrate specialisation and also the greatest amount of substrate species were *Bjerkandera adusta* (35 recorded total substrate genera; mostly with beech (49%), birch (14%) and oak (11%)) and *Trametes versicolor* (34 recorded substrate genera; predominantly associated with beech (28%), birch (22%) and oak (17%)).

While fungal species with epithets signifying their substrate affinity could be often associated with those trees – for example, *Lenzites betulina* (13 total recorded substrate genera) had a 67% affinity to birch, some were more misleading in terms of associations in the UK (but could be based on other regions, e.g., the prevalence of *Picea abies* in Scandinavia, or due to tree decline, e.g., the loss of *Ulmus* in the UK) – such as *Trichaptum abietinum* (14 total

genera), that had 81% of occurrences with pine and 0.4% with fir (*Abies*), and *Rigidoporus ulmarius* (14 total genera) with only 40% of occurrences with elm (*Ulmus*) and 11% with maple (*Acer*)).

The Polyporales dominated the wood decay fungi in this UK study, and were found across all degrees of substrate affinity. In comparison, fewer wood decay species were found in the Hymenochaetales and Russulales, which demonstrated mid-level to specialist substrate affinities. This corresponded with a greater amount of white rot fungi with low substrate affinity, while brown rot fungi had exclusively mid- to high affinity levels with specific woody substrate genera (Figure 1; Supplemental Table 1). Fungi of both rot types were associated with both deciduous angiosperms and conifers, especially the Fagales (beech, oak, birch and hornbeam (*Carpinus*)) and the Pinaceae (pine (*Pinus*), spruce (*Picea*), larch (*Larix*), and fir (*Abies*)). Fungal species with greater affinity to pine were often also associated with spruce and larch at levels equalling and greater than to those of the Fagales taxa, i.e., the suggestion for conifer preference. The fungal species with lowest substrate affinities were always annually fruiting white rot fungi in association with dead, downed wood. For the woody genera, the horticultural and hedgerow shrub-like taxa (e.g., *Ligustrum*) and trees with peeling to flaking bark (e.g., *Platanus*) were the rarest substrates for the wood decay fungi.

There was a positive correlation between genetic distances among fungal species and their host distribution; hence, phylogenetically related species shared more of the same host taxa ($p \leq 0.008$). The significance of the Procrustes analysis ($p \leq 0.005$) suggested a very low probability of the correlation being the result of random effects.

Compositional changes on substrates by time, region and climate

Substrate genera accounted for a major part of the variation in fungal assemblies (31.5%; Table 1). In the CCA, composition sorted largely by wood type of the substrates along the first axis (angiosperm versus conifer wood; Figure 2). The fungal composition also aligned with substrate taxonomy and host growth form, i.e., those communities associated with trees in the Fagales were more similar to one another, and in terms of the angiosperm taxa, they arranged most distally from the horticultural and shrub-like taxa. The second CCA axis gradient differentiated fungal compositions within the angiosperm tree substrates, and less that of the conifer substrates. Hence, while the second axis primarily captured variation in fungal assemblies across deciduous substrates, the first axis captured that between the types of woody genera, as well as within the conifer group (Figure 2). For example, medium- to high affinity brown rot fungi were mostly associated with the conifer and Fagales- associated communities.

Compared to the host genera, climate variability accounted for a very small part of the variation in fungal assemblies (Table 1). Among the assessed climate variables, mean annual temperature was the most important, still, it only accounted for 0.4% of the variation in fungal composition (Table 1). Temperature functioned simultaneously (i.e., non-linearly) between the two gradients, as illustrated by the isolines in the CCA plot, encompassing the fungal communities of both wood type groupings in annual means of 8.6 to 9.4 °C, with some suggestion for climate trends within-groupings of conifer and Fagales associations (Figure 2).

The compositional variance by decade (1970's to 2000's) and region (eastern or western UK) constituted 1.7% of the overall variability, which was conditioned from the host and climate-focused effects on composition. In fact, compositional variance that had been related to the decade (1970's to 2000's) and region (eastern or western UK) were so minimal that the eight

decade-region combinations were as effective to display as averages (Figure 2), but see Supplemental Figure 2 for the non-averaged version.

Influence of fungal traits and climate on substrate usage

The fourth-corner and RLQ analyses were used to test associations between fungal traits and habitat characteristics based on the compositional trends. There was a positive association between fungal spore volume and species having angiosperm trees as substrate (Table 2). There were also associations between rot type and substrate, with white rot taxa preferentially appearing on angiosperm substrates ($p \leq 0.00$) and brown rot taxa on coniferous substrates. A trend for relatively more occurrences on downed deadwood (as opposed to standing) occurred across the four decades (adj. $p \leq 0.05$).

Fungal species' trait-mediated changes in abundance between earlier (1970 – 1990) and later (1991 – 2010) decades were impacted by the substrate stage (lying deadwood versus standing wood; Supplemental Table 2 & Supplemental Table 3). For fungi of both substrate types and after accounting for recorder effort, models indicated an increase in species from the first to the second time period (Figure 3). Importantly, the trends were parallel for the two substrate types, suggesting no bias and equal increases in abundances. In contrast, when considered in terms of relative percent increase, the mean expected substrate value was disproportionately higher with time, predicting more fungi on fallen deadwood compared to standing substrate.

Discussion

Our three objectives related to quantifying the degree of substrate affinity by wood decay fungi (including taxa in the Polyporales, Hymenochaetales, Russulales, and Thelephorales). We questioned how this might be influential to climate- and temporal- related change of fungi on their substrates. The records of wood decay fungi in this study originated from multiple sources (mainly citizen science records and research studies) of fruit body records limited to the UK for the 1970 to 2000's decades.

We (1) found that specialization occurred for fungi across rot types, while generalization was restricted to white rot fungi. Fungi were mostly restricted to fallen deadwood if their substrate affinity was low, while the frequency of fungi on standing trees increased with higher substrate affinities. Fungal species more often exhibited substrate affinity classifiable by characteristics of angiosperm or conifers. There were (2) also discernible compositional patterns, where woody substrate genera arranged primarily along gradients clustering conifers and angiosperm substrate characteristics, with temperature gradients only in minor part interacting within these more dominant compositional forces. Among the trait-related trends, a positive relationship between fungal species composition by rot type and substrate type (angiosperm or conifer) was detected, again evidencing the importance of substrate characteristics that relate to wood properties in structuring composition. Across the four decades, the fungal species composition shifted on downed deadwood due to a positive association with it, in contrast to the lack of any correlation with species composition on standing wood. This corroborated our final finding (3) where models indicated more fungi on downed deadwood than standing substrate across time.

Our results suggest that substrate shifts by wood decay fungi may be mediated to some extent by climate change (as defined in this case by broad geographical trends of eastern and western UK), but are primarily determined by woody hosts, related to their general wood properties, for example, angiosperms or conifers. Substrate shifts by fungi on downed deadwood will be the most challenging to discern, as they are primarily generalists in affinity (Supplemental Table 1), and can also be infrequent and patchily distributed within wood, based on molecular evidence (Baldrian et al. 2016). That fungi were modelled to have increased (relatively) more on deadwood than standing substrate in the latter half of the time period added further challenge in discerning causes for trends. We could only speculate whether management programmes towards coarse woody debris retainment contributed to this trend.

We were originally most interested in the potential for substrate shifts by taxa with higher substrate affinity within the UK, for example as has been found for *Auricularia auricula-judae* (Gange et al. 2011; 2012; Boddy et al. 2014). One interpretation is that our results demonstrate the potential for considerable plasticity in even the most host-specific taxa (Figure 1), as no species was singularly observed on one host genus. This could make sense in terms of the structure and chemical composition of wood primarily differentiating between angiosperm and conifers (e.g., Miller 1999) than nuances between species. It does also explain the results we report here, in that species' substrate affinity and compositional patterns related foremost to wood properties, and only very limited extent to climate (Table 1, Figure 2). Recently Leonhardt et al. (2018) demonstrated, somewhat similarly, distinction in wood decay fungi by tree leaf type (deciduous or evergreen), and when combined with further results, pinpointed the ligninolytic manganese peroxidase enzymatic pathway as influential for explaining fungal substrate differences. Even more recently Runnel et al. (2021) likewise dissected differences in polypores related to Estonian forest biodiversity.

Potential biases must always be borne in mind when trying to interpret these data. For example, are rare substrate reports for fungal species clearly specialising on certain tree taxa genuine or misidentifications? Instances have been found where people tended towards reporting the more unusual sightings of fungal fruiting, for example, when out of season or on an unusual host (Halme et al. 2016). However, as in other cases, is there observer bias (e.g., Heilmann-Clausen et al. 2019), or even unknown effects of cryptic speciation (e.g., Runnel et al. 2021) impacting the results? Our analytical approach cannot answer these questions. In the future, more certainty could be obtained where there is access to vouchers connected to the records for molecular investigations alongside morphological comparisons for species assessment (e.g., Andrew et al. 2018d).

Heilmann-Clausen et al. (2016) also, through citizen science data, investigated more than 1000 fungal species and 91 woody substrate genera in Denmark. They showed that substrate tree size, wood pH, and the number of species within each substrate genus to positively influence fungal wood decay species richness. This concurs with our findings that properties of the wood, and decay type, are the bases for differences in the substrate affinity of fungi. We again suggest that experiments on the growth of fungi in different wood types, both alone and competing with others, and environmental cues for fruiting (Moore et al. 2008), are needed to elucidate this further. Substrate affinity of fungal species may also vary depending on environment (Boddy et al. 2014), and our results demonstrated that mean annual temperature was more influential than annual precipitation in structuring communities.

Future studies in different regions, time periods or other spatiotemporal scales, would benefit from focusing separately on angiosperm or conifer wood, so as to more clearly discern

impacts of climate on fungal decay, which are clearly lesser to that of biotic associations (Figure 2). Our results, and those of Heilmann-Clausen et al. (2016) match well with those found using molecular methodologies (Baldrian et al. 2016; Leonhardt et al. 2018; Purahong et al. 2018a; 2018b), indicating the value of both approaches.

Conclusion

Substrate affinity, in the strictest sense, is less frequent than generalization for wood decay species. Greater affinity is more likely to occur with fungi associated with standing wood than for those on downed wood, and the latter are more often generalist white rot fungi. Substrate shifts are likely to be exacerbated in conditions that change the presence of wood decay taxa, properties related to wood types (angiosperm or conifer) and substrate location (standing versus downed dead), and, to a very limited extent, climate when defined by mean annual temperature. It would be extremely beneficial to continue to characterize fungal affinities across other regions than those discussed here, to determine the actual mechanisms related to fungal decay affinity (which would better distinguish degree of affinity), and to assess any impacts that new biotic associations, resultant from substrate shifts, may have on extant fungal communities and their dynamics.

Conflicts of interest

All authors affirm that no competing interests exist with respect to this manuscript.

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Authors' contributions (listed alphabetically by last name)

CJA, LB, ACG, EH, KH, HK, FR conceived of and participated in the design of the study.

CJA, EH, HK, FR conducted the statistical analyses.

CJA, LB, ACG, EH, KH, HK, FR drafted the manuscript.

All authors gave final approval for publication.

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Figure and Table captions

Figure 1: The proportional occurrences (log10) of fungal species on woody substrate genera are color-coded from none (lightest beige) to approaching complete specificity (darkest maroon). Fungal species are ordered from the most general to the most specific substrate affinities to the woody genera listed. The substrate genera are ordered from high (left) to low (right) numbers of fungal species. The dendrogram for the fungal species is accompanied by shading of general rot type (brown versus white), and for the substrate genera by their wood types (broad-leaved angiosperm versus needle-leaved conifer).

Figure 2: The compositional similarity between the fungal species recorded in associate with woody substrate genera. Each abbreviation represents the fungal composition associated with a substrate genus (the three letters), averaged across the four decades and two regions for clarity. The woody substrate genera are shaded by their wood type, broad-leaved angiosperm (lighter green) or needle-leaved conifer (darker green), which differentiate the fungal compositions. The greyscale numbers represent the fungal species' scores relative to the substrate communities, i.e., species influencing neighbouring communities. The fungal species are ordered (1 to 61) in increasing substrate affinity. The grey shadings reflect the species' general rot-type (brown versus white). Mean annual temperature, which explains less compositional variability than does the substrate genus, is non-linearly associated with compositional variance and is represented by the orange isolines. See Figure 1 for the full substrate genera names as well as the fungal species names in order of substrate affinities. See Table 1 for the extent of variance explained by habitat variables. Figure 2 is the matching, the more detailed plot version that includes fungal communities by decade and region.

690 Table 1: Variance partitioning of climate (mean annual temperature) and substrate (woody
691 genera) from the CCA analysis. The model is spatiotemporally conditioned by four decades
692 (1970's to 2000's) and region (eastern or western UK), which contributed <2% variance.
693
694 Table 2: The statistically significant correlations in the fungal traits related to the
695 compositional variability are shown with respect to the associated habitat characteristics
696 (woody substrate and environmental properties). The directions of the relationships were
697 always positive, as noted by the plus signs, which designate the degree of statistical
698 significance. The adjusted p-value is also reported in the parentheses (adj. $p \leqslant$ value).
699
700 Figure 3: Modelled absolute (A) and relative change (B) in fungal observations by time (1970
701 – 1990 versus 1991 – 2010) depends upon the substrate type, i.e. downed deadwood versus
702 standing wood. For both substrate types, the total number of fungal observations are predicted
703 to increase with time, but the relationship between the use of host stages remains relatively
704 stable, i.e., parallel responses. In contrast, the relative percent change between the substrates
705 is proportionally different, demonstrating that downed deadwood is favoured with time.