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

3

4 Fredrik Rustøen ^a, Klaus Høiland ^a, Einar Heegaard ^b, Lynne Boddy ^c, Alan C. Gange ^d, Håvard
5 Kauserud ^a, Carrie Andrew ^{a, e}

6

7 ^a Section for Genetics and Evolutionary Biology (EVOGENE), University of Oslo,
8 Blindernveien 31, 0316, Oslo, Norway

9 ^b Forestry and Forest Resources, Norwegian Institute of Bioeconomy Research, Fanaflaten 4,
10 N-5244, Fana, Norway

11 ^c School of Biosciences, Cardiff University, Museum Avenue, Cardiff CF10 3AX, United
12 Kingdom

13 ^d Department of Biological Sciences Royal Holloway, University of London, Egham, Surrey
14 TW20 0EX, United Kingdom

15 ^e Oberlin College & Conservatory, Biology Department, 119 Woodland Street, Oberlin, Ohio,
16 US, 44074

17

18

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

20 **Abstract**

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

33

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

35 **Introduction**

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

46

47 The timing of fruit body production is different to that of half a century ago for many species
48 (Boddy et al. 2014; Andrew et al. 2018b), and the shifts are direct consequences of climate
49 (Andrew et al. 2018c). For example, in southern England the average fruiting period of 315
50 fungal species has more than doubled from 33.2 ± 1.6 d to 74.8 ± 7.6 d in the timespan of
51 1950 to 2005 (Gange et al. 2007). Kauserud et al. (2008) likewise demonstrated a similar
52 pattern in Norway, when investigating the phenology of 83 agaricoid species. By utilizing
53 large fungarium datasets of records from 1940 to 2006, they detected a delay in fungal
54 fruiting by 13.3 ± 1.2 d across all species. While it is unquestionable that climate change is a
55 cause of fungal phenological shifts (Andrew et al. 2018c), less clear is how the degree of
56 affinity of fungi to their substrates might interact with climate-based impacts (Boddy et al.
57 2014).

58

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

71

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

82

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

93
94 Dynamics of wood decay fungi indicate that priority effects (Ottosson et al. 2014; Hiscox et
95 al. 2015; 2016; Leopold et al. 2017; Norberg et al. 2019) as well as competitive interactions
96 (van der Wal et al. 2016; Hiscox et al. 2018) shape communities and successional change.
97 Wood properties are also important, for example wood chemistry (Fukasawa 2021; Lunde et
98 al. 2022), decay stage (Holec et al. 2020) and stem diameter (Brazee et al. 2012). Less clear at
99 this point, however, is the degree that fungal affinity, i.e., specialization to specific substrate
100 taxa, might influence and inter-relate to climate effects.

101

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

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

113

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

124

125 **Materials and Methods**

126 *Data filtering and processing*

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

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

144

145 A variety of climate variables were investigated for potential trends, entirely and across two
146 equal time periods (1970-1990 and 1991-2010). Data were obtained from the Met Office in
147 2016, and overlain with a Watsonian vice-county map (a geographical division of the British
148 Isles for the purpose of scientific data collection). The geography of the UK contributed to a
149 longitudinal climate gradient that we used to divide, as appropriate for analyses, the climate
150 and fungal data into two (multivariate) and eight (regression) zones (Supplemental Figure 1).
151 Temperature (minimum, maximum and mean), and precipitation (total) were investigated at
152 both annual and seasonal (meteorological spring, summer, autumn, and winter) aggregations.
153 Mean annual temperature between the years and regions ranged from 8.07 to 9.65 °C, while
154 maximum annual temperatures ranged from 11.34 to 13.43 °C, and minimum annual
155 temperatures from 4.77 to 5.75 °C. Annual rainfall ranged from 746.11 to 1501.95 mm.

156

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

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

186

187 The 28S LSU genetic distance data were correlated with a Simpson index of variation in
188 substrate distributions among the fungal species, calculated as the difference in the Simpson
189 1-D index values between the species, to understand if genetic similarity related to substrate
190 usage. The degree that genetic distance and the substrate-diversity distances matched was
191 estimated with a Pearson correlation across all interspecific comparisons. We investigated
192 how linear transformations of one matrix matched the other matrix with Procrustes analyses
193 (package *vegan* in R; Oksanen et al. 2016). A large residual difference of the matrices would
194 indicate a poor match between the genetic and Simpson index differences. The Procrustes
195 analyses results were further verified through a permutation test (999 permutations) with a
196 null-hypothesis that the Simpson index was independently distributed among the fungal
197 species. The diversity distance matrix was recalculated for each species from permuted values
198 and compared to the original genetic distances. If the observed correlation and Procrustes
199 match was high, the permuted absolute correlation was assumed lower, and the residuals of
200 the Procrustes larger. From these results, the correlation in genetic similarity and substrate
201 usage was determined.

202

203 *Compositional changes by substrate, time, region and climate*

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

207 1980s, 1990s, 2000s), and the associated climate (mean annual temperature and precipitation).
208 Little difference in fungal species composition on substrate genera between regions or
209 decades would suggest few spatiotemporal changes in substrate specificities, hence little
210 substrate specificity based on the prevailing climatic conditions. Greater compositional
211 differences would, on the other hand, suggest substrate specificity changes for fungi on
212 certain substrate genera.

213

214 By investigating the composition of decay fungi associated with woody substrate genera, we
215 were able to examine the potential of climate-related shifts of fungi on their substrates, and in
216 relation to spatiotemporal variance. We utilized canonical-correlation analysis (CCA)
217 combined with variance partitioning. The compositional variability was dissected by the
218 extent the available variables explained it, either individually or when confounded (Borcard et
219 al. 2011). Forward selection of the 23 original Met Office variables identified the four
220 variables that were included in the final analyses (mean annual temperature, decadal time
221 period, region, and substrate genus). Four decadal time periods (1970's, 1980's, 1990's, and
222 2000's) and two climate-driven regions (eastern and western UK; Supplemental Figure 1)
223 were selected. To reduce any possible effects of different sampling efforts between regions,
224 the data were transformed to presence-absence of fungal species per substrate, region and
225 time period. Two substrate genera (*Euonymus* and *Ribes*) and the one fungal species that
226 associated most often with them, *Phylloporia ribis*, were outliers and were subsequently
227 removed from the analyses. The variance attributable to spatiotemporal effects was
228 constrained in the CCA, so as to focus upon the dominating impacts of climate and substrate
229 genera.

230

231 *Influence of fungal traits and climate on substrate usage*

232 A fourth-corner and RLQ analysis explained how fungal traits on a compositional level
233 related to the fungal habitat, i.e., plot-level variables of environment and substrate (Dray et al.
234 2014). The variables as previously selected in the CCA and variance partitioning analyses
235 were included. A correspondence analysis was run for the continuous variables. A Hill-Smith
236 analysis was utilized on matrices with both categorical and continuous variables (Brown et al.
237 2014; Dray et al. 2014). Randomization procedures implemented 49,000 permutations and the
238 *P* values were adjusted for multiple testing with the false discovery rate procedure (Dray et al.
239 2014). From these analyses, directional correlations were generated based on the trait trends
240 in the fungal species composition by those of the habitat variables.

241

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

254

255 **Results**

256 *Substrate specializations*

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

265

266 Further species that were recorded on few substrate genera, but which demonstrated less
267 specificity, were (Figure 1; Supplemental Table 1): *Hericium erinaceus* with 4 recorded
268 substrate genera, but 92% of occurrences with beech (*Fagus*); *Hericium cirrhatum* with 7
269 recorded substrate genera, but 83% of occurrences with beech; and *Corioloopsis gallica* which
270 was associated with 5 recorded substrate genera, although 50% of occurrences were with
271 beech and 39% with ash (*Fraxinus*). The species with overall less substrate specialisation and
272 also the greatest amount of substrate species were *Bjerkandera adusta* (35 recorded total
273 substrate genera; mostly with beech (49%), birch (14%) and oak (11%)) and *Trametes*
274 *versicolor* (34 recorded substrate genera; predominantly associated with beech (28%), birch
275 (22%) and oak (17%)).

276

277 While fungal species with epithets signifying their substrate affinity could be often associated
278 with those trees – for example, *Lenzites betulina* (13 total recorded substrate genera) had a
279 67% affinity to birch, some were more misleading in terms of associations in the UK (but
280 could be based on other regions, e.g., the prevalence of *Picea abies* in Scandinavia, or due to
281 tree decline, e.g., the loss of *Ulmus* in the UK) – such as *Trichaptum abietinum* (14 total

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

285

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

300

301 There was a positive correlation between genetic distances among fungal species and their
302 host distribution; hence, phylogenetically related species shared more of the same host taxa (p
303 ≤ 0.008). The significance of the Procrustes analysis ($p \leq 0.005$) suggested a very low
304 probability of the correlation being the result of random effects.

305

306 *Compositional changes on substrates by time, region and climate*

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

319

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

327

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

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

334

335 *Influence of fungal traits and climate on substrate usage*

336 The fourth-corner and RLQ analyses were used to test associations between fungal traits and
337 habitat characteristics based on the compositional trends. There was a positive association
338 between fungal spore volume and species having angiosperm trees as substrate (Table 2).

339 There were also associations between rot type and substrate, with white rot taxa preferentially
340 appearing on angiosperm substrates ($p \leq 0.00$) and brown rot taxa on coniferous substrates. A
341 trend for relatively more occurrences on downed deadwood (as opposed to standing) occurred
342 across the four decades (adj. $p \leq 0.05$).

343

344 Fungal species' trait-mediated changes in abundance between earlier (1970 – 1990) and later
345 (1991 – 2010) decades were impacted by the substrate stage (lying deadwood versus standing
346 wood; Supplemental Table 2 & Supplemental Table 3). For fungi of both substrate types and
347 after accounting for recorder effort, models indicated an increase in species from the first to
348 the second time period (Figure 3). Importantly, the trends were parallel for the two substrate
349 types, suggesting no bias and equal increases in abundances. In contrast, when considered in
350 terms of relative percent increase, the mean expected substrate value was disproportionately
351 higher with time, predicting more fungi on fallen deadwood compared to standing substrate.

352 **Discussion**

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

359

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

375

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

386

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

401
402 Potential biases must always be borne in mind when trying to interpret these data. For
403 example, are rare substrate reports for fungal species clearly specialising on certain tree taxa
404 genuine or misidentifications? Instances have been found where people tended towards
405 reporting the more unusual sightings of fungal fruiting, for example, when out of season or on
406 an unusual host (Halme et al. 2016). However, as in other cases, is there observer bias (e.g.,
407 Heilmann-Clausen et al. 2019), or even unknown effects of cryptic speciation (e.g., Runnel et
408 al. 2021) impacting the results? Our analytical approach cannot answer these questions. In the
409 future, more certainty could be obtained where there is access to vouchers connected to the
410 records for molecular investigations alongside morphological comparisons for species
411 assessment (e.g., Andrew et al. 2018d).

412
413 Heilmann-Clausen et al. (2016) also, through citizen science data, investigated more than
414 1000 fungal species and 91 woody substrate genera in Denmark. They showed that substrate
415 tree size, wood pH, and the number of species within each substrate genus to positively
416 influence fungal wood decay species richness. This concurs with our findings that properties
417 of the wood, and decay type, are the bases for differences in the substrate affinity of fungi.
418 We again suggest that experiments on the growth of fungi in different wood types, both alone
419 and competing with others, and environmental cues for fruiting (Moore et al. 2008), are
420 needed to elucidate this further. Substrate affinity of fungal species may also vary depending
421 on environment (Boddy et al. 2014), and our results demonstrated that mean annual
422 temperature was more influential than annual precipitation in structuring communities.

423
424 Future studies in different regions, time periods or other spatiotemporal scales, would benefit
425 from focusing separately on angiosperm or conifer wood, so as to more clearly discern

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

430

431 **Conclusion**

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

443

444 **Conflicts of interest**

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

446

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453

454 **Authors' contributions (listed alphabetically by last name)**

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

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

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

458 All authors gave final approval for publication.

459 **References**

460 Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier,
461 M., ... & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality
462 reveals emerging climate change risks for forests. *Forest ecology and Management*, 259, 660-
463 684.

464

465 Andrew, C., Halvorsen, R., Heegaard, E., Kuyper, T. W., Heilmann - Clausen, J., Krisai -
466 Greilhuber, I., ... & Kirk, P. M. (2018a). Continental - scale macrofungal assemblage patterns
467 correlate with climate, soil carbon and nitrogen deposition. *Journal of Biogeography*, 45,
468 1942-1953.

469

470 Andrew, C., Heegaard, E., Gange, A. C., Senn-Irlet, B., Egli, S., Kirk, P. M., ... & Boddy, L.
471 (2018b). Congruency in fungal phenology patterns across dataset sources and scales. *Fungal*
472 *Ecology*, 32, 9-17.

473

474 Andrew, C., Heegaard, E., Høiland, K., Senn - Irlet, B., Kuyper, T. W., Krisai - Greilhuber,
475 I., ... & Bässler, C. (2018c). Explaining European fungal fruiting phenology with climate
476 variability. *Ecology*, 99, 1306-1315.

477

478 Andrew, C., Diez, J., James, T. Y., & Kausserud, H. (2018d). Fungarium specimens: a largely
479 untapped source in global change biology and beyond. *Philosophical Transactions of the*
480 *Royal Society B*, 374(1763), 20170392.

481

482 Baldrian, P., Zrůstová, P., Tláškal, V., Davidová, A., Merhautová, V., & Vrška, T. (2016).
483 Fungi associated with decomposing deadwood in a natural beech-dominated forest. *Fungal*
484 *Ecology*, 23, 109-122.
485
486 Bien, S., & Damm, U. (2020). Prunus trees in Germany—a hideout of unknown fungi?.
487 *Mycological Progress*, 19, 667-690.
488
489 Boddy, L., Büntgen, U., Egli, S., Gange, A. C., Heegaard, E., Kirk, P. M., ... & Kauserud, H.
490 (2014). Climate variation effects on fungal fruiting. *Fungal Ecology*, 10, 20-33.
491
492 Borcard, D., Gillet, F., & Legendre, P. (2018). *Numerical ecology with R*. Springer.
493
494 Brazeo, N. J., Lindner, D. L., Fraver, S., D'Amato, A. W., & Milo, A. M. (2012). Wood-
495 inhabiting, polyporoid fungi in aspen-dominated forests managed for biomass in the US Lake
496 States. *Fungal Ecology*, 5, 600-609.
497
498 Breitenbach, J., & Kränzlin, F. (1986). *Fungi of Switzerland, Vol. 2. Non gilled fungi-*
499 *Heterobasidiomycetes, Aphyllophorales, Gasteromycetes. Fungi of Switzerland, Vol. 2. Non*
500 *gilled fungi-Heterobasidiomycetes, Aphyllophorales, Gasteromycetes.*
501
502 Brown, A. M., Warton, D. I., Andrew, N. R., Binns, M., Cassis, G., & Gibb, H. (2014). The
503 fourth - corner solution - using predictive models to understand how species traits interact
504 with the environment. *Methods in Ecology and Evolution*, 5, 344-352.
505

506 Cao, Y., Larsen, D. P., & Thorne, R. S. J. (2001). Rare species in multivariate analysis for
507 bioassessment: some considerations. *Journal of the North American Benthological Society*,
508 20, 144-153.

509

510 Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary
511 climate change. *Science*, 292, 673-679.

512

513 Diez, J., Kauserud, H., Andrew, C., Heegaard, E., Krisai-Greilhuber, I., Senn-Irlet, B., ... &
514 Büntgen, U. (2020). Altitudinal upwards shifts in fungal fruiting in the Alps. *Proceedings of*
515 *the Royal Society B*, 287, 20192348.

516

517 Dray, S., & Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for
518 ecologists. *Journal of Statistical Software*, 22, 1-20.

519

520 Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & ter Braak, C.
521 J. (2014). Combining the fourth - corner and the RLQ methods for assessing trait responses to
522 environmental variation. *Ecology*, 95, 14-21.

523

524 Floudas, D., Held, B. W., Riley, R., Nagy, L. G., Koehler, G., Ransdell, A. S., ... & Hibbett,
525 D. S. (2015). Evolution of novel wood decay mechanisms in Agaricales revealed by the
526 genome sequences of *Fistulina hepatica* and *Cylindrobasidium torrendii*. *Fungal Genetics and*
527 *Biology*, 76, 78-92.

528

529 Fukasawa, Y. (2021). Ecological impacts of fungal wood decay types: a review of current
530 knowledge and future research directions. *Ecological Research*, 36, 910-931.

531

532 Gange, A. C., Gange, E. G., Sparks, T. H., & Boddy, L. (2007). Rapid and recent changes in
533 fungal fruiting patterns. *Science*, 316, 71-71.

534

535 Gange, A. C., Gange, E. G., Mohammad, A. B., & Boddy, L. (2011). Host shifts in fungi
536 caused by climate change? *Fungal Ecology*, 4, 184-190.

537

538 Gange, A. C., Gange, E. G., Mohammad, A. B., & Boddy, L. (2012). Fungal host shifts: bias
539 or biology?. *Fungal Ecology*, 5, 647-650.

540

541 Halme, P., Heilmann-Clausen, J., Rämä, T., Kosonen, T., & Kunttu, P. (2012). Monitoring
542 fungal biodiversity—towards an integrated approach. *Fungal Ecology*, 5(6), 750-758.

543

544 Heilmann-Clausen, J., & Læssøe, T. (2012). On species richness estimates, climate change
545 and host shifts in wood-inhabiting fungi. *Fungal Ecology*, 5, 641-646.

546

547 Heilmann-Clausen, J., Maruyama, P. K., Bruun, H. H., Dimitrov, D., Læssøe, T., Frøslev, T.
548 G., & Dalsgaard, B. (2016). Citizen science data reveal ecological, historical and evolutionary
549 factors shaping interactions between woody hosts and wood - inhabiting fungi. *New*
550 *Phytologist*, 212, 1072-1082.

551

552 Hiscox, J., Savoury, M., Müller, C. T., Lindahl, B. D., Rogers, H. J., & Boddy, L. (2015).
553 Priority effects during fungal community establishment in beech wood. *The ISME Journal*, 9,
554 2246-2260.

555

556 Hiscox, J., Savoury, M., Johnston, S. R., Parfitt, D., Müller, C. T., Rogers, H. J., & Boddy, L.
557 (2016). Location, location, location: priority effects in wood decay communities may vary
558 between sites. *Environmental Microbiology*, 18, 1954-1969.

559

560 Hiscox, J., O'leary, J., & Boddy, L. (2018). Fungus wars: basidiomycete battles in wood
561 decay. *Studies in Mycology*, 89, 117-124.

562

563 Holec, J., Kučera, T., Běťák, J., & Hort, L. (2020). Macrofungi on large decaying spruce
564 trunks in a Central European old-growth forest: what factors affect their species richness and
565 composition?. *Mycological Progress*, 19, 53-66.

566

567 Heilmann-Clausen, J., Bruun, H. H., Ejrnæs, R., Frøslev, T. G., Læssøe, T., & Petersen, J. H.
568 (2019). How citizen science boosted primary knowledge on fungal biodiversity in
569 Denmark. *Biological Conservation*, 237, 366-372.

570

571 Jamil, T., Ozinga, W. A., Kleyer, M., & ter Braak, C. J. (2013). Selecting traits that explain
572 species–environment relationships: a generalized linear mixed model approach. *Journal of*
573 *Vegetation Science*, 24, 988-1000.

574

575 Kauserud, H., Stige, L. C., Vik, J. O., Økland, R. H., Høiland, K., & Stenseth, N. C. (2008).
576 Mushroom fruiting and climate change. *Proceedings of the National Academy of Sciences*,
577 105, 3811-3814.

578

579 Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate
580 change. *Proceedings of the National Academy of Sciences*, 105, 11823-11826.

581

582 Leonhardt, S., Hoppe, B., Stengel, E., Noll, L., Moll, J., Bässler, C., ... & Kellner, H. (2019).

583 Molecular fungal community and its decomposition activity in sapwood and heartwood of 13

584 temperate European tree species. *PloS one*, 14, e0212120.

585

586 Leopold, D. R., Wilkie, J. P., Dickie, I. A., Allen, R. B., Buchanan, P. K., & Fukami, T.

587 (2017). Priority effects are interactively regulated by top - down and bottom - up forces:

588 evidence from wood decomposer communities. *Ecology Letters*, 20, 1054-1063.

589

590 Lunde, L. F., Jacobsen, R., Kauserud, H., Boddy, L., Nybakken, L., Sverdrup-Thygeson, A.,

591 & Birkemoe, T. (2022). Legacies of invertebrate exclusion and tree secondary metabolites

592 control fungal communities in dead wood. *Molecular Ecology*, 31, 3241-3253.

593

594 Miller, R.B. (1999). Structure of Wood. Chapter 2. *From: Forest Products Laboratory*. 1999.

595 Wood handbook—Wood as an engineering material. Gen. Tech. Rep. FPL–GTR–113.

596 Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory.

597 463 p.

598

599 Moore, D., Gange, A. C., Gange, E. G., & Boddy, L. (2008). Fruit bodies: their production

600 and development in relation to environment. In *British Mycological Society Symposia Series*,

601 Vol. 28, 79-103. Academic Press.

602

603 Norberg, A., Halme, P., Kotiaho, J. S., Toivanen, T., & Ovaskainen, O. (2019).

604 Experimentally induced community assembly of polypores reveals the importance of both

605 environmental filtering and assembly history. *Fungal Ecology*, 41, 137-146.

606

607 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... &
608 Stevens, M. H. H. (2016). *vegan: Community Ecology Package*. R package version 2.4-3.
609 Vienna: R Foundation for Statistical Computing.

610

611 Ottosson, E., Nordén, J., Dahlberg, A., Edman, M., Jönsson, M., Larsson, K. H., ... &
612 Ovaskainen, O. (2014). Species associations during the succession of wood-inhabiting fungal
613 communities. *Fungal Ecology*, 11, 17-28.

614

615 Pachauri, R. K., Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., ... & Dubash,
616 N. K. (2014). *Climate change 2014: synthesis report. Contribution of Working Groups I, II
617 and III to the fifth assessment report of the Intergovernmental Panel on Climate Change (p.
618 151)*. Ippc.

619

620 Purahong, W., Wubet, T., Krüger, D., & Buscot, F. (2018a). Molecular evidence strongly
621 supports deadwood-inhabiting fungi exhibiting unexpected tree species preferences in
622 temperate forests. *The ISME Journal*, 12, 289-295.

623

624 Purahong, W., Wubet, T., Lentendu, G., Hoppe, B., Jariyavidyanont, K., Arnstadt, T., ... &
625 Bauhus, J. (2018b). Determinants of deadwood-inhabiting fungal communities in temperate
626 forests: molecular evidence from a large scale deadwood decomposition experiment. *Frontiers
627 in Microbiology*, 9, 2120.

628

629 Renvall, P. (1995). Community structure and dynamics of wood-rotting Basidiomycetes on
630 decomposing conifer trunks in northern Finland. *Karstenia*, 35, 1-51.

631

632 Riley, R., Salamov, A. A., Brown, D. W., Nagy, L. G., Floudas, D., Held, B. W., ... &
633 Grigoriev, I. V. (2014). Extensive sampling of basidiomycete genomes demonstrates
634 inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proceedings of the*
635 *National Academy of Sciences*, 111, 9923-9928.

636

637 Ripley, B. (2011). MASS: support functions and datasets for Venables and Ripley's MASS. R
638 package version, 7, 3-29.

639

640 Runnel, K., Miettinen, O., & Lõhmus, A. (2021). Polypore fungi as a flagship group to
641 indicate changes in biodiversity—a test case from Estonia. *IMA fungus*, 12(1), 1-31.

642

643 Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent
644 Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal*
645 *Statistical Society: Series b (statistical methodology)*, 71, 319-392.

646

647 Ryvarden, L., & Melo, I. (2014). Poroid fungi of Europe. *Fungiflora*.

648

649 Schmidt, O. (2006). *Wood and tree fungi* (pp. 334). Springer-Verlag Berlin Heidelberg.

650

651 Song, Z., Kennedy, P. G., Liew, F. J., & Schilling, J. S. (2017). Fungal endophytes as priority
652 colonizers initiating wood decomposition. *Functional Ecology*, 31, 407-418.

653

654 Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. (2011). MEGA5:
655 molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance,
656 and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731-2739.

657

658 van der Wal, A., Klein Gunnewiek, P. J., Cornelissen, J. H. C., Crowther, T. W., & de Boer,
659 W. (2016). Patterns of natural fungal community assembly during initial decay of coniferous
660 and broadleaf tree logs. *Ecosphere*, 7, e01393.

661

662 Wollan, A. K., Bakkestuen, V., Kauserud, H., Gulden, G., & Halvorsen, R. (2008). Modelling
663 and predicting fungal distribution patterns using herbarium data. *Journal of Biogeography*, 35,
664 2298-2310.

665 **Figure and Table captions**

666

667 Figure 1: The proportional occurrences (\log_{10}) of fungal species on woody substrate genera
668 are color-coded from none (lightest beige) to approaching complete specificity (darkest
669 maroon). Fungal species are ordered from the most general to the most specific substrate
670 affinities to the woody genera listed. The substrate genera are ordered from high (left) to low
671 (right) numbers of fungal species. The dendrogram for the fungal species is accompanied by
672 shading of general rot type (brown versus white), and for the substrate genera by their wood
673 types (broad-leaved angiosperm versus needle-leaved conifer).

674

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

689

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. $p \leq$ 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.