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1 Relationships between macro-fungal dark diversity and 2 habitat parameters using LiDAR

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12 Abstract

13 Despite the important role of fungi for ecosystems, relatively little is known about the factors
14 underlying the dynamics of their diversity. Moreover, studies do not typically consider their
15 dark diversity: the species absent from an otherwise suitable site. Here, we examined
16 potential drivers of local fungal dark diversity in temperate woodland and open habitats using
17 LiDAR and in-situ field measurements, combined with a systematically collected and
18 geographically comprehensive macro-fungi and plant data set. For the first time, we also
19 estimated species pools of fungi by considering both plant and fungi co-occurrences. The
20 most important LiDAR variables for modelling fungal dark diversity were amplitude and
21 echo ratio, which are both thought to represent vegetation structure. These results suggest that
22 the local fungal dark diversity is highest in production forests like plantations and lowest in
23 more open forests and in open habitats with little woody vegetation. Plant species richness
24 was the strongest explanatory factor overall and negatively correlated with local fungal dark
25 diversity. Soil fertility showed a positive relationship with dark diversity in open habitats.
26 These findings may indicate that the local dark diversity of macro-fungi is highest in areas
27 with a relatively high human impact (typically areas with low plant species richness and high
28 soil fertility). Overall, this study brings novel insights into local macro-fungi dark diversity
29 patterns, suggesting that a multitude of drivers related to both soil and vegetation act in
30 concert to determine fungal dark diversity.

31 **Key Words:** airborne laser scanning, bog, fens, forests, fungal diversity, grasslands,
32 mycorrhiza, regional species pool, remote sensing, shrublands, wetlands

33 **Introduction**

34 Understanding the underlying drivers shaping biodiversity patterns is a central goal in
35 ecology and conservation biology. This is also true for fungi which play a vital role in
36 ecosystem functioning as decomposers, mutualists, and pathogens. However, fungi and the
37 underlying environmental factors influencing fungal diversity is less studied than animals and
38 plants, and quantifying fungal diversity is far from trivial. The most commonly used
39 biodiversity metric is observed species richness (Mueller 2011). However, this measure is not
40 always suitable for comparisons across habitats and conveys no information on the part of the
41 diversity that is potentially missing in a given site (Pärtel *et al.* 2011). In addition, monitoring
42 fungal diversity is often severely hampered by detectability issues and the life history of the
43 involved species (Yahr *et al.* 2016, Blackwell and Vega 2018). Several alternative
44 approaches have been developed to more effectively monitor and compare biodiversity across
45 landscapes (Solow and Polasky 1994, Sarkar and Margules 2002, Ricotta 2005, Ricotta
46 2007). Although these methods can provide valuable insights, they do not consider the dark
47 diversity, the absent part of the species pool which can potentially inhabit an environmentally
48 suitable site (Pärtel *et al.* 2011). This often-ignored aspect of diversity provides a novel and
49 ecologically meaningful metric for estimating how much of the potential species diversity –
50 the site-specific species pool – is lacking (Pärtel *et al.* 2011). This information is important to
51 understand the underlying mechanisms and dynamics of community assembly (e.g.,
52 community saturation) (Mateo *et al.* 2017). Dark diversity may also become an important
53 conservation tool to measure biodiversity potential, such as aiding managers or policy-makers
54 to prioritize certain habitats, estimate restoration potential of degraded habitats, or forecast
55 potential impacts of invasions (Lewis *et al.* 2017). Here, we use fungal data from 130
56 thoroughly inventoried sites covering all terrestrial habitats, from open to forest, and wet to
57 arid, to investigate important drivers of fungal dark diversity.

58 Dark diversity aims to reconcile the role of simultaneous, and potentially
59 confounding, regional and local processes underlying biodiversity patterns and biological
60 communities (Pärtel *et al.* 2011, Pärtel 2014). In any given landscape, the biodiversity
61 potential is ultimately determined by large-scale biogeographic and evolutionary processes
62 (i.e., species diversification and historic migration patterns) determining the set of species

63 which can theoretically inhabit a site, defined as the regional pool (Pärtel *et al.* 1996, Cornell
64 and Harrison 2014, Zobel 2016). This regional pool is further filtered by local processes such
65 as environmental gradients, species interactions, population dynamics, dispersal, disturbance,
66 and stochastic events and referred to as the site-specific species pool, i.e., species that could
67 possibly live in a given site (Pärtel *et al.* 2013, Cornell and Harrison 2014, Ronk *et al.* 2015,
68 Zobel 2016). While many studies have investigated the drivers of fungal diversity, only a few
69 studies have focused on the determinants of fungal dark diversity. These studies demonstrate
70 that higher temperatures increases arbuscular mycorrhizal dark diversity (Pärtel *et al.* 2017a)
71 and annual precipitation decreases the dark diversity of ectomycorrhizal fungi at the global
72 scale (Pärtel *et al.* 2017b). These results concur with previous research suggesting that large
73 scale climatic factors are strong drivers of fungal richness and community composition,
74 attributed to the direct and indirect effects which alter soil and floristic conditions (Staddon *et*
75 *al.* 2003, Kivlin *et al.* 2011, Tedersoo *et al.* 2014). Local edaphic conditions such as soil
76 moisture, pH, and calcium concentration are also known to influence fungal diversity (Geml
77 *et al.* 2014, Tedersoo *et al.* 2014, Tonn and Ibáñez 2017, Frøslev *et al.* 2019), but it is not
78 known how these environmental factors affect fungal dark diversity. In fact, the general
79 mechanisms determining dark diversity in fungal communities remain largely unknown.
80 Clearly, species can be absent from an area just by chance (Hubbell 2011). Species can also
81 be absent from a site because of some kind of unexpected disturbance – for example human,
82 but it could also be natural – altering species’ dispersal, establishment, or persistence
83 possibilities. In principle, these disturbances can be both biological and chemical and act at
84 various spatial scales. An example could be extreme drought. Often habitats have a constant
85 level of relatively low or usual disturbances that the habitat’s species are adapted to (e.g.,
86 grazing), and these do not count towards disturbances that can cause dark diversity. It is
87 important not to confuse dark diversity with hidden diversity; i.e., species that are actually
88 present in a given site but just not recorded (Milberg *et al.* 2008, Abrego *et al.* 2016).

89 Besides the influence of environmental gradients, other factors particularly important
90 for fungi are vegetation and habitat structure, such as vegetation height, shrub layer,
91 vegetation cover, dead wood, and other woody features (Humphrey *et al.* 2000, Nordén and
92 Paltto 2001, Nordén *et al.* 2004, Gómez-Hernández and Williams-Linera 2011, Zuo *et al.*
93 2016). As the dominant primary producer in terrestrial ecosystems, plants also form the living
94 and dead organic carbon pools and biotic surfaces that are the niche space for not only fungi
95 but other taxonomic groups as well (DeAngelis 2012, Brunbjerg *et al.* 2017). These structural

96 elements are an important element for biodiversity, and can influence not only fungal
97 diversity, but the diversity of plants, animals, and bacteria as well (Penone *et al.* 2019).
98 However, despite the obvious contribution of these variables, such factors are rarely covered
99 extensively since they are difficult to measure and require large amounts of resources to
100 obtain sufficient and high quality data. However, emerging technologies such as LiDAR
101 (light detection and ranging) could potentially remedy this situation.

102 Airborne LiDAR records a three-dimensional set of points using laser ranging from an
103 aircraft or a drone (Lefsky *et al.* 2002). It captures data suitable to represent many of the
104 vegetation and landscape structural measures important to fungi (Vehmas *et al.* 2009, Lopatin
105 *et al.* 2016, Peura *et al.* 2016, Thers *et al.* 2017, Mao *et al.* 2018). As a relatively new
106 methodology, biodiversity studies that employ LiDAR have been limited in scope, typically
107 addressing only one taxonomic group or habitat type at the local scale, and strongly biased
108 towards forest ecosystems. However, studies using LiDAR-based indicators have already
109 been shown to explain up to 66% and 82% of local plant and fungi richness, respectively
110 (Lopatin *et al.* 2016, Peura *et al.* 2016, Thers *et al.* 2017). A recent study has demonstrated its
111 potential to provide spatially accurate and comprehensive measures by predicting the local
112 biodiversity of different taxonomic groups (plants, fungi, lichens, and bryophytes) across
113 multiple habitat types and large geographic extent (Moeslund *et al.* 2019). LiDAR may also
114 be a useful tool in studying dark diversity by incorporating potentially important
115 spatiotemporal dynamics such as succession and disturbance (Mokany and Shine 2003, Scott
116 *et al.* 2011, Pärtel *et al.* 2013). For example, recent studies have found that human impact
117 increases dark diversity in arbuscular mycorrhizal fungi (Pärtel *et al.* 2017a), that ruderal
118 plants are more likely to be in dark diversity (Moeslund *et al.* 2017), and that human density
119 and agricultural land-use influence dark diversity of vascular plants (Riibak *et al.* 2017).

120 Alongside these structural and environmental factors, fungal diversity depends on
121 biotic interactions, with a large proportion of fungi deriving their nutrients and carbon from
122 host plants (Tedersoo *et al.* 2014, Nguyen *et al.* 2016). Recent evidence has hinted on the
123 influence of these interactions on dark diversity, as plant species dependent on mycorrhiza
124 have been found to have greater dark diversity than those without these mutualist
125 relationships (Moeslund *et al.* 2017). Moreover, ectomycorrhizal fungal diversity seems to
126 increase exponentially with an increasing proportion of their host plants, suggesting that
127 competitive interactions among fungi might also drive their dark diversity (Pärtel *et al.*
128 2017b). Typical and strong species interactions are indeed typically considered in dark

129 diversity, as the estimation hereof is usually based on species co-occurrences (Beals 1984,
130 McCune 1994, Münzbergová and Herben 2004, de Bello *et al.* 2012, Lewis *et al.* 2016).
131 However, this is usually done only within the species group being studied. For example, in
132 studies of plant dark diversity, only co-occurrences with other plants, and not fungi or other
133 species groups, are typically considered. However, recognizing the close and interconnected
134 relationship between plants and fungi allows for stronger and more realistic estimations of the
135 fungal dark diversity. Incorporating other taxonomic groups when determining species pools
136 and estimating dark diversity is not a new insight, and the importance of biotic interactions
137 across trophic groups has been discussed since the concept of dark diversity was first
138 introduced (Pärtel *et al.* 2011). Yet, such cross-species group data has never been included in
139 dark diversity estimates meaning that they may not sufficiently account for cross-species
140 group interactions, and this may be part of the explanation for why dark diversity is
141 sometimes over-estimated (Boussarie *et al.* 2018).

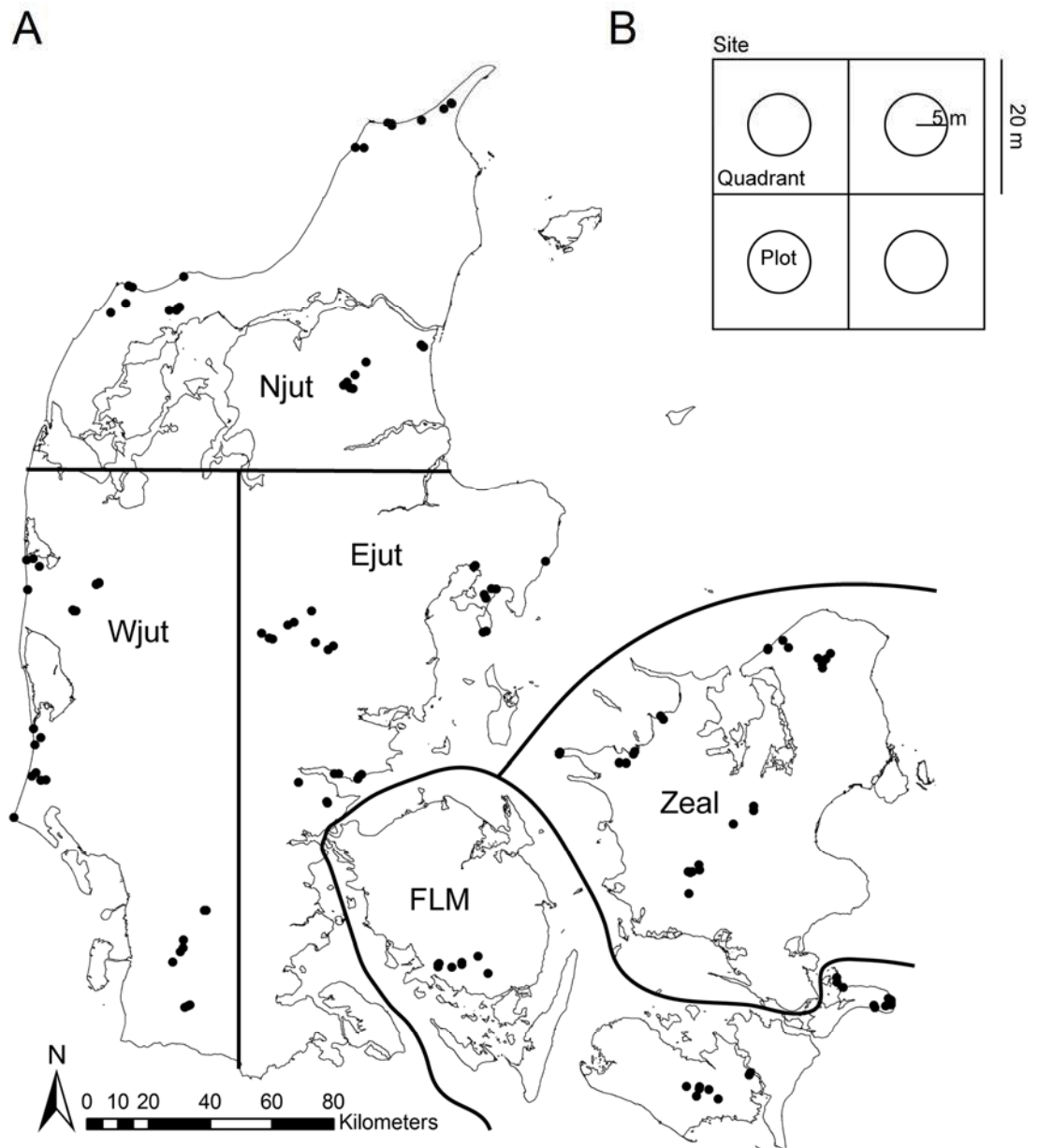
142 In this study, we examined a number of environmental factors influencing the local
143 dark diversity of fungi across habitat-types nationwide within Denmark. We used a
144 comprehensive biodiversity datasets covering major environmental gradients (Brunbjerg *et al.*
145 *et al.* 2019) and combined it with LiDAR-based measurements. We also included fungi-plant-
146 co-occurrence information to estimate local fungal dark diversity and thereby acknowledge
147 the importance of their biotic interactions. More specifically, we addressed the following
148 questions: 1. To what degree can we explain local fungal dark diversity by abiotic and biotic
149 environmental factors? 2. Can vegetation and terrain structural factors that are important to
150 local fungal dark diversity be derived from LiDAR and if so, 3. how important are they
151 compared to field-measured factors?

152 **Methods**

153 *Study area and site selection*

154 The dataset was collected from a national biodiversity inventory in Denmark as part
155 of the “Biowide” research project (Brunbjerg *et al.* 2019). A total of 130 study sites (40 × 40
156 m) were selected with a minimum distance of 500 m between each to reduce spatial
157 covariance with 30 sites allocated to cultivated habitats and 100 sites to natural habitats
158 (Figure 1). The cultivated subset was stratified according to the type of land use and the
159 natural subset was selected amongst uncultivated habitats and stratified according to
160 gradients in soil fertility, soil moisture, and successional stage. The “Biowide” project

161 deliberately excluded saline and aquatic habitats but included temporarily inundated
162 depressions along with mires, bogs, and fens. The final set of 24 habitat strata consisted of
163 three types of fields (rotational, grass leys, set aside) and three types of plantations (beech,
164 oak, spruce), and the remaining 18 strata were natural or semi-natural habitats, constituting
165 all possible combinations of positions along three major natural environmental gradients: soil
166 fertility (rich, poor), soil moisture (dry, moist, wet), and successional stage (early, mid, late).
167 These 24 strata were replicated in five geographical regions in Denmark. The “Biowide”
168 dataset also includes a subset of 10 sites (two in each region) of hotspots for different
169 taxonomic groups in Denmark, which were selected by voting amongst active naturalists in
170 the Danish conservation and management societies. For further details on the design and data
171 collection procedures see Brunbjerg *et al.* (2019).



172
173 Figure 1. The (A) 130 selected study sites from a national biodiversity inventory and (B) the
174 four quadrants and 5m circle plots within each site. Reprinted from Ejrnæs *et al.* (2018),
175 with permission from Elsevier.

176 *Field-measured variables*

177 We used fungi observational data from the “Biowide” field inventories (summarized
178 data and additional details in Brunbjerg *et al.* (2019)). Macro-fungal species were surveyed in
179 2014–2015 by an expert field-mycologist and volunteers during three inventories (up to one

180 hour per site) in the main fruiting season (August - November) by actively searching
181 microhabitats and substrates (soil, herbaceous vegetation and debris, dead wood, litter, and
182 bark of trees up to 2 m) within the 40 × 40 m sites. Since truffles are difficult to find, we did
183 not consider these in this study. Subspecies and varieties were lumped to the species level.
184 After pre-processing, the dataset consisted of 6,269 observations of 1,017 species.

185 Vascular plant species observations were also taken from the “Biowide” database and
186 were originally inventoried by trained botanists during the summer 2014 and spring 2015 to
187 account for variations in phenology. We removed hybrids and neophytes (i.e. species that are
188 not considered a natural part of the vegetation given their history and dispersal ability, see
189 appendix tables 6–8 in Buchwald *et al.* (2013)) and lumped subspecies and varieties to the
190 species level. Species nomenclature for both plants and fungi follow the species checklist of
191 Denmark (allearter.dk).

192 Apart from the LiDAR-based measures (detailed below), we also considered field-
193 measured variables representing both abiotic conditions and available biotic resources known
194 to influence fungal diversity and communities (Table 1). For further details on data collection
195 and how the environmental field measurements were made see Brunbjerg *et al.* (2019).

196 Table 1. Overview of the explanatory variables for fungal dark diversity models along with our hypothesized relationship with dark
 197 diversity. If the standard deviation of a variable was calculated, in addition to its mean, the variable is denoted with an asterisk.

| | Explanatory variables | Hypothesis | References |
|-------------------------|--|---|---|
| Field-based measures | Plant richness | High plant richness could mean higher community stability or reflect low human impact. This would result in a lower dark diversity | (Kuiters 2013, Pellkofer <i>et al.</i> 2016, Yang <i>et al.</i> 2018) |
| | Litter (open habitats) and dead wood (forests) | The more substrate represented by more organic matter gives more resources for fungi and hence a lower dark diversity. Alternatively, organic matter increases competition between fungi and soil bacteria or causes many unfilled microhabitats which would increase dark diversity | (Leigh <i>et al.</i> 2011, Averill <i>et al.</i> 2014) |
| | Soil pH | Despite increasing importance of bacteria and invertebrates in decomposition with increasing soil pH, we also expect less dominance and better opportunities for fungal colonization as the base-rich soil environment is less restrictive, where only few species can cope with low pH values, possibly resulting in a lower dark diversity at high pH | (Clark 1997, Rousk <i>et al.</i> 2009, Rousk <i>et al.</i> 2010) |
| | Soil fertility index (SFI) | Asymmetric competition among vascular plants | (Buckland and Grime 2000, Liu <i>et</i> |

| | | | |
|----------------------|---------------------------|---|---|
| | | increases with increasing soil fertility leading to loss of plant richness at high fertility levels and therefore potentially also increasing dark diversity | <i>al.</i> 2015, Nadeau and Sullivan 2015, Luo <i>et al.</i> 2017) |
| | Soil moisture index (SMI) | Most fungi thrive at intermediate soil moisture levels, but have a rapid and opportunistic growth response to high moisture. Assuming establishment is easier in intermediate moist environments dark diversity could be higher at high moisture. Alternatively, dark diversity could be high at intermediate moisture levels as this could yield many unfilled microhabitats | (Jacobson 1997, Kennedy and Peay 2007) |
| LiDAR-based measures | Vegetation height* | Taller vegetation could reflect encroachment by shrubs and trees in open habitats and forests resulting in more available microhabitats for potential fungal species increasing their dark diversity | (Zuo <i>et al.</i> 2016, Gómez <i>et al.</i> 2019) |
| | Succession (Amplitude) | Amplitude could reflect successional processes with later successional stages allowing fungi to become more established, resulting in lower dark diversity | (Fernández-Toirán <i>et al.</i> 2006, Twieg <i>et al.</i> 2007, Hui <i>et al.</i> 2017) |

| | | |
|--|--|--|
| <p>Microtopography</p> <ul style="list-style-type: none"> -Terrain roughness (SigmaZ) -Terrain openness* | <p>Microtopography increases availability of microhabitats and hence could increase dark diversity</p> | <p>(Cantelmo Jr and Ehrenfeld 1999)</p> |
| <p>Light/heat</p> <ul style="list-style-type: none"> - Canopy openness (forests)* -Heat load index* -Solar irradiation* -Vegetation cover* | <p>Light availability increases fungal establishment success which would decrease dark diversity</p> | <p>(Graham <i>et al.</i> 1982, Turner <i>et al.</i> 2009)</p> |
| <p>Canopy complexity</p> <ul style="list-style-type: none"> -Echo ratio* | <p>Canopy complexity provides more niches directly in the canopy and could also be expected to be associated with a higher variation in the forest floor with small openings in the canopy and variation in tree ages. This could increase the number of unfilled microhabitats and hence the dark diversity</p> | <p>(Unterseher and Tal 2006, Gómez-Hernández and Williams-Linera 2011, Dove and Keeton 2015)</p> |

198 ***LiDAR-based measures***

199 To enable the calculation of measures representing vegetation and terrain environmental
200 and structural aspects, we used the latest nationally covering LiDAR-based point cloud for
201 Denmark from the Danish Ministry of Environment. This dataset is freely available from
202 www.kortforsyningen.dk and has a point density of 4-5 points/m². Originally, this dataset was
203 recorded from fixed-wing airplanes at an altitude of approximately 680 m above ground level
204 and a speed over ground of approximately 240 km/h. The data was recorded by Riegl LMS-680i
205 scanners operating in the near-infrared wavelength (1550 nm) in a parallel line scan pattern
206 during the springs and autumns of 2014 and 2015. For all calculations, we relied on the
207 classification of points into ground, building and vegetation classes already present in the data
208 set upon download.

209 To represent vegetation and terrain environmental and structural aspects, we calculated
210 observed measures based on the point cloud data set. We calculated all measures at 1.5 m
211 resolution (except for terrain roughness which was at 0.5 m resolution) and their means and
212 standard deviations within 30 m radius circles centered in each study site. For all LiDAR
213 processing and calculation, we used the OPALS tools (Pfeifer *et al.* 2014) version 2.3.1 in a
214 Python 2.7 environment.

215 ***Vegetation-related measures***

216 To represent *succession* and to some degree moisture balance in both vegetation and soil,
217 we used the amplitude of each echo representing a point in the LiDAR point cloud. This
218 amplitude is high if the reflecting surface is flat (i.e., smooth) and with high reflectivity. It is low
219 when the light energy is distributed between several returns for example in tree canopies, or
220 when surfaces have low reflectivity, are complex, or translucent (e.g., leaves). The wavelength
221 used to record the point cloud data is sensitive to leaf water content (Junttila *et al.* 2018) and soil
222 moisture (Zlinszky *et al.* 2014). Since the amplitude depends on reflectivity, which varies across
223 months and aircraft types (slightly different flying heights) used for data recording, the amplitude
224 was corrected to account for these biases. We constructed a Generalized Linear Model (GLM)
225 with Gaussian link having the raw amplitude as response and flight month as well as aircraft type
226 as explanatory factors and used only the residuals of this model for input in our statistical
227 modelling. We also tried using flight year as an explanatory factor, but this did not improve the

228 model ($\Delta AIC < 2$). These residuals will be referred to as the *corrected amplitude* in the
229 following. Unfortunately, we did not have reference data enabling a full calibration of this
230 measure (Höfle and Pfeifer 2007).

231 To represent *vegetation height*, we estimated this measure by subtracting the terrain
232 model from the surface model (two raster files, detailed in the following). The terrain model
233 (DTM) calculation details are given in the section on “Terrain-structure measure”. The surface
234 model was calculated using the DSM module in OPALS using all vegetation and ground points.

235 To reflect the penetrability and succession of the vegetation we calculated the *echo ratio*
236 (Höfle *et al.* 2012). Echo ratio is high where the surface is impenetrable and relatively smooth
237 and lower where the surface is uneven or penetrable. In order to calculate the echo ratio,
238 estimating normals for each point is required. We did this using the Normals module in OPALS
239 with a robust plane fit based on the 12 nearest neighboring points. Subsequently, we calculated
240 the echo ratio for each terrain and vegetation point using a search radius of 1.5 m along with the
241 slope adaptive method implemented in the EchoRatio module of OPALS.

242 To estimate light conditions, we calculated the *canopy openness* for all points categorized
243 as “ground”, but contrary to terrain openness (see below), we calculated this considering
244 vegetation points as well. Therefore, canopy openness represents the actual blocking of the sky
245 view by the canopy around each ground point. Canopy openness is high for ground points inside
246 canopy gaps and low for ground points beneath a closed canopy.

247 Lastly, as an estimate of *vegetation cover*, we calculated the fraction of vegetation points
248 to all points (excluding unclassified points and those representing buildings and noise). This
249 measure will be high if the vegetation is dense or the cover of vegetation is relatively high, and
250 low for areas with no vegetation.

251 *Terrain-structure measures*

252 To enable the calculation of several terrain-related measures, we calculated a digital
253 terrain model (DTM) for each study site representing the elevation above sea level. To do this we
254 used the DTM module of OPALS based on only ground points. We set the module to use 8
255 neighboring points and a search radius of 6 m. To represent key features of the local terrain (e.g.,
256 soil moisture or heat balance (Moeslund *et al.* 2013)), we calculated *terrain slope* and *terrain*

257 *aspect* (used for heat load index calculation, see below). For this task, we used the GridFeature
258 module of OPALS using the DTM as input, a kernel size of 1 and requesting the terrain slope
259 and aspect (slope direction) in radians.

260 To reflect local heat input, we calculated the *heat load index* based on the terrain aspect
261 following the heat load index formula in McCune and Keon (2002). This index reaches
262 maximum values on southwest-facing slopes and zero on northeast-facing slopes. We also
263 calculated the potential *solar irradiation* based on terrain slope, aspect, and latitude following
264 equation 3 in McCune and Keon (2002).

265 To estimate micro-scale terrain heterogeneity, we calculated the *terrain roughness*
266 (SigmaZ) using only ground points as input. This measure represents the standard deviation of
267 the interpolated grid height. The OPALS DTM module outputs this measure as a by-product
268 when constructing a DTM. However, unlike the rest of the LiDAR measures in this study, the
269 terrain roughness was calculated at 0.5×0.5 m resolution mirroring micro-scale terrain
270 variations.

271 To represent site-scale terrain heterogeneity, we calculated the *terrain openness* (Doneus
272 2013). Terrain openness is defined as the opening angle of a cone (having the radius of the
273 kernel) turned upside down – with its tip restrained to the point of interest – that touches the
274 terrain surface. To calculate this, we used the PointStats module of OPALS requesting “positive
275 openness” based on only ground points and a search radius of 5 m. This measure is high in flat
276 (relative to the scale at which it is calculated) areas and low in heterogeneous terrains.

277 Finally, to test the importance of variability in the LiDAR measures we calculated the
278 standard deviation for LiDAR measures for which we believed it made ecological sense (Table
279 1).

280 ***Data analysis***

281 *Data preparation*

282 Prior to statistical analysis, we removed the six intensively managed fields from the study
283 sites, as these were ploughed fields. We also removed two study sites because they were flooded
284 during the LiDAR data recording period. Finally, we removed one site due to an extreme outlier

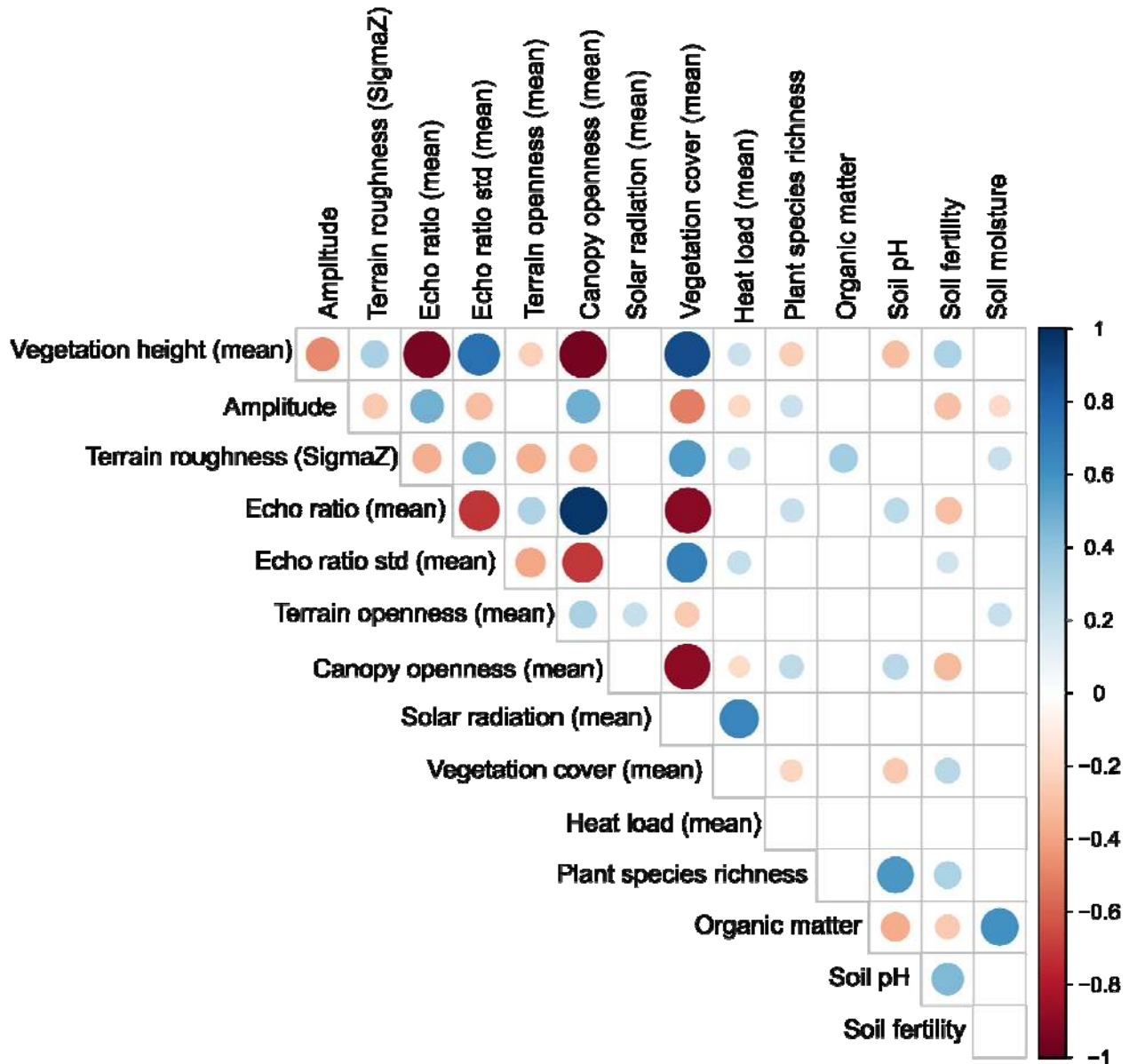
285 in the LiDAR amplitude values (300 vs. a range of values between 10 and 130). Our final dataset
286 therefore comprised a total of 121 study sites.

287 Our initial visual inspection of the data revealed that many of the LiDAR measures were
288 relevant only for woodlands and therefore strongly zero-inflated in the open landscapes. The
289 analyses in this study were therefore separately run for open habitats and woodlands. Open
290 habitats included grasslands, fens, bogs, and other habitats with only few sporadic occurrences of
291 trees. The woodlands dataset consisted of forests, thickets and shrubland (e.g. willow).

292 In the following, we detail the steps we took to prepare the LiDAR and measured
293 variables for statistical modelling as explanatory factors. Obviously, a number of these variables
294 were strongly inter-correlated (Appendix 1). For example, echo ratio was strongly related to
295 canopy and light measures (Appendix 1). Therefore, we selected only those variables that we
296 hypothesized to affect local fungal dark diversity (See Table 1). Subsequently, to avoid issues
297 with multi-collinearity we calculated Variance Inflation Factors (VIFs) causing us to remove
298 vegetation height as an explanatory factor for the open landscapes to ensure VIF values below 10
299 following Kutner *et al.* (2005). Subsequently, the maximum VIF value of explanatory factors
300 used together in the same models was 4.8 and 5.7 for woodlands and open habitats respectively.
301 We scaled all explanatory variables to a mean of zero and a standard deviation of one. To strive
302 for normal distribution of explanatory variables we log- or square-root transformed those where
303 this made obvious distributional improvements based on visual examination of the histograms.

304

305 **Appendix 1.** Correlation plot between environmental and LiDAR variables. All significant
 306 interactions are colored red for negative relationships and blue for positive relationships, with the
 307 size and darkness of the color representing the strength of the relationship. Non-significant
 308 correlations are blank.



309

310

311 Dark diversity

312 All statistical analyses mentioned in the following were performed in R version 3.5.3 (R
 313 Core Team 2019). To calculate the dark diversity for each site, we first calculated the site-
 314 specific species pool using the Beals' index (Beals 1984), as recommended by Lewis *et al.*

315 (2016), using the ‘beals’ function in the ‘vegan’ package (Oksanen *et al.* 2017). The Beals’ index
316 represents the probability that a particular species will occur within a given site based on the
317 assemblage of co-occurring species (Beals 1984, McCune 1994, Münzbergová and Herben
318 2004). The threshold used for including a particular species in the site-specific species pool was
319 the 5th percentile of the Beals’ index value for each species (Gijbels *et al.* 2012, Ronk *et al.*
320 2015). Preceding the calculation of each threshold, the lowest Beals’ index value among plots
321 with the occurrence of the species in question was identified, and all plots having values below
322 the minimum were not considered. We calculated two measures of the site-specific species pool
323 for each site: (1) using only fungi co-occurrence and (2) co-occurrences of both observed fungi
324 and vascular plants at each site to acknowledge the fungal-plant linkages (i.e., both fungi and
325 plant species were in the presence/absence matrix used to calculate Beals’ index). Dark diversity
326 was calculated by subtracting observed fungal species richness from the site-specific species
327 pool. Since site-specific species pools differ between sites, we calculated the *relative dark*
328 *diversity* for each site as dark diversity (species predicted from the site-specific species pool but
329 not observed) divided by the regional pool to enable comparison of results across habitats.

330 Statistical analysis

331 To investigate what characterizes sites with a high fungal dark diversity we constructed
332 GLMs with a Gaussian link having the estimated relative dark diversity (described above) as the
333 response variable. We constructed models for both open habitats and woodlands, and for both
334 dark diversity estimates (see the section on dark diversity). Initially, we fitted models using only
335 the LiDAR measures as explanatory factors, to test the degree to which fungal dark diversity
336 patterns could be explained using LiDAR data alone. Subsequently, we fitted a similar model
337 with both measured and LiDAR variables as explanatory factors (Table 1), giving insight into
338 how much more explanatory power one gains by using measured variables in addition to LiDAR.
339 To allow for non-linear relationships for variables corresponding to the intermediate disturbance
340 hypothesis (Connell 1978, Townsend *et al.* 1997) and intermediate productivity hypothesis
341 (Fraser *et al.* 2015), we used Akaike’s Information Criterion (AIC) (Burnham and Anderson
342 2002) to evaluate if inclusion of squared terms for the variables SMI, SFI, light, soil pH, and
343 bare soil (see Table 1) improved the model fit. If so, we kept the squared term of the variable in
344 question instead of the linear effect. After the initial fit and checking for non-linearity as

345 described above, we ran a backward model selection procedure for each model based on AIC.
346 The procedure stopped when AIC did not drop anymore and Δ AIC was above 2 (Burnham and
347 Anderson 2002). In each iteration, we dropped the variable causing the smallest change in AIC
348 value. As a final step, we checked model residuals to ensure that these were normally distributed.
349 We did not conduct spatial modelling in this study, since the original field-work design lying
350 behind the data was designed to avoid spatial autocorrelation, and tests for all the species groups
351 originally inventoried concluded that spatial signals were of minor to little importance (see
352 Brunbjerg *et al.* (2019), and also “Study area and site selection”).

353 **Results**

354 The two relative fungal dark diversity estimates (based on fungi-only and both fungi- and
355 plant co-occurrences) were between 0.17 – 0.93 (open habitats, median 0.51) and 0.20 – 0.63
356 (woodland, median: 0.39); and 0.21 – 0.95 (open habitats, median: 0.56) and 0.24 – 0.7
357 (woodland, median: 0.44) respectively. In most cases, our models explained between 20-30 % of
358 the variation in fungal dark diversity and more than 40 % for the woodlands models when
359 including both LiDAR and measured variables (Table 2). In the “fungi-only dark diversity”
360 model for woodland habitats (Table 2) the squared term of soil pH did improve model fit, but
361 this term was left out during the subsequent model selection procedure.

362 The only LiDAR variable significant in both open habitats and woodlands was amplitude,
363 which was significant in all models for woodlands and in LiDAR-only models for open habitats
364 (Table 2). This variable had a positive effect on dark diversity in woodlands (Table 2) but a
365 negative influence in open habitats (Table 2). Echo ratio was the only other significant LiDAR
366 variable in our analyses and positively influenced dark diversity in open habitats (Table 2). Plant
367 richness was negatively related to local fungal dark diversity and had the strongest impact of all
368 the field-measured factors included in our analyses (Table 2). Also, soil fertility and moisture
369 were positively correlated with fungal dark diversity in open habitats (Table 2).

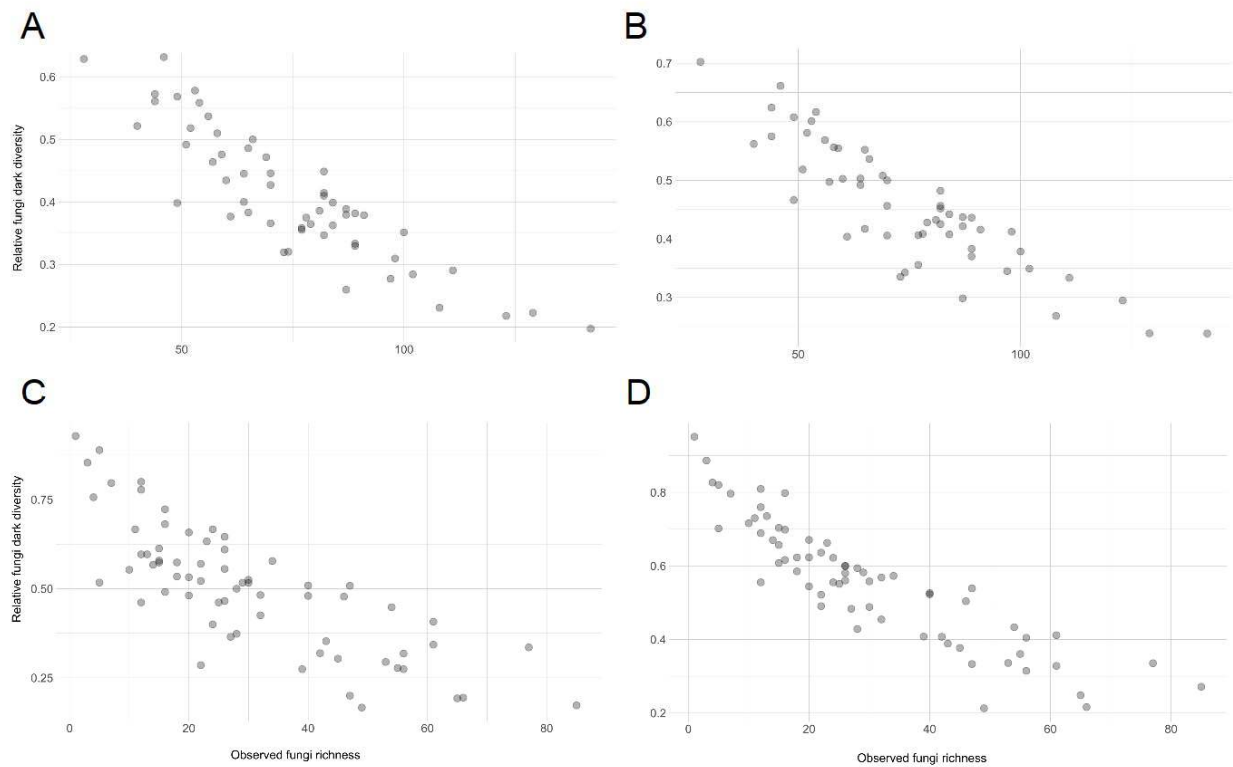
370 In all cases, models considering only the structural environment (LiDAR only) were
371 outperformed by models considering plant richness and the abiotic environment in addition to
372 the structural, notably in the open habitats (Table 2). Appendix 1 shows all pair-wise Spearman
373 correlations between the explanatory variables used and Appendix 2 shows observed fungi
374 richness against the two dark diversity measures for both open and woodland habitats.

375

376 Table 2. Modelling coefficients for the best models (i.e. after model selection) regressing dark diversity estimates based on only fungi
 377 co-occurrences (*Fungi-only dark diversity*) or based on both fungi and plant co-occurrences (*Fungi-plant dark diversity*) against the
 378 selected explanatory variables. Significant variables were from either a LiDAR-only or a full model with both LiDAR-based and field-
 379 measured predictors.

| | | | LiDAR variables | | | Field-measured variables | | |
|-------------------|----------------------------|------------------|-----------------|-----------|------------|--------------------------|----------------|---------------|
| | | | R ² | Amplitude | Echo ratio | Plant richness | Soil fertility | Soil moisture |
| Woodland habitats | Fungi-only dark diversity | Lidar-only model | 0.24 | 0.03 | - | - | - | - |
| | | Full model | 0.40 | 0.04 | - | -0.05 | - | - |
| | Fungi-plant dark diversity | Lidar-only model | 0.23 | 0.03 | - | - | - | - |
| | | Full model | 0.44 | 0.04 | - | -0.05 | - | - |
| Open habitats | Fungi-only dark diversity | Lidar-only model | 0.10 | -0.05 | 0.01 | - | - | - |
| | | Full model | 0.30 | - | 0.01 | -0.08 | 0.06 | 0.04 |
| | Fungi-plant dark diversity | Lidar-only model | 0.07 | -0.04 | 0.01 | - | - | - |
| | | Full model | 0.34 | - | 0.01 | -0.10 | 0.06 | - |

380 **Appendix 2.** Relationship between observed fungal diversity and dark diversity estimates in
381 woodland based on (A) only fungi co-occurrences (*Fungi-only dark diversity*) or (B) fungi and
382 plant co-occurrences (*Fungi-plant dark diversity*), and in open habitats based on (C) only fungi
383 co-occurrences (*Fungi-only dark diversity*) or (D) fungi and plant co-occurrences (*Fungi-plant*
384 *dark diversity*).



385

386 Discussion

387 In this study, we demonstrate for the first time that LiDAR derived variables, alone and
388 in combination with field-measured variables, can explain a significant amount of the variation
389 in local dark diversity of temperate macro-fungal communities. Our findings indicate that the
390 dark diversity of fungi is influenced by the local vegetation structure, plant associations, and the
391 abiotic environment. This is not surprising since local observed fungal diversity is also
392 determined by these factors to a large degree (Thers *et al.* 2017, Yang *et al.* 2017, Moeslund *et*
393 *al.* 2019). Indeed, the relative dark diversity analyzed in this study correlated with the observed
394 fungal species richness (Appendix 2), which was expected given that the dark diversity
395 calculations are based on the species present (Noreika *et al.* 2020). On the other hand, there are

396 differences between these two measures, so the results presented here are not necessarily
397 applicable to the observed fungal diversity. We also find that models including field-based
398 variables explained the dark diversity of fungi far better than models relying solely on LiDAR,
399 notably in open landscapes. While LiDAR has the advantage that one can record data from huge
400 areas in very fine detail for relatively low cost, our results indicates that to get the best
401 explanation of local fungal diversity patterns fieldwork is still needed.

402 *LiDAR-based measures*

403 This study shows that LiDAR captures habitat characteristics potentially important for
404 fungal dark diversity which are not represented by traditional field-measured variables. Notably,
405 the relationship between fungal dark diversity and LiDAR-derived vegetation structure in
406 woodlands was relatively strong. Although LiDAR can successfully quantify biophysical
407 characteristics in all types of habitats, it is known to be more effective in forested habitats (Su
408 and Bork 2007), supporting these findings. The most important LiDAR variables for modelling
409 fungal dark diversity were amplitude and echo ratio which gives us important insights into what
410 environmental aspects, which are not typically recorded in field-surveys, can be captured by a
411 LiDAR approach.

412 The LiDAR measure of amplitude is sensitive both to surface reflectivity and to the
413 number of targets hit by the laser pulse (Moeslund *et al.* 2019). The lower the reflectivity and the
414 more targets between which the light energy is distributed, the lower the amplitude associated
415 with a given point. This would result in high amplitudes in flatter surfaces while yielding low
416 amplitudes in tall and more complex canopies, or translucent surfaces such as leaves. Hence, this
417 variable can be a proxy for succession stage, surface evenness, or vegetation density; since both
418 flat and sparsely vegetated as well as densely vegetated canopies preventing light penetration
419 will yield high amplitude. Supporting this, amplitude was positively correlated with vegetation
420 height and vegetation cover (denser vegetation resulted in higher amplitude) and negatively
421 correlated with echo ratio (vegetation complexity, see below) and canopy openness. In
422 woodlands, the dark diversity of fungi was positively related to amplitude, suggesting that more
423 species are missing in the relatively tall and dense forests compared to more complex woodlands
424 (e.g., with canopy openings). The positive association between LiDAR amplitude and dark
425 diversity could therefore be a consequence of communities in older well-developed shrubland or

426 old-growth forests with windthrows or other openings, having allowed fungi more time to
427 become established with their associated plants (Fernández-Toirán *et al.* 2006, Twieg *et al.*
428 2007). Indeed, among the top half of woodland plots with regards to amplitude were plantations
429 (which often have dense canopy and equal-aged trees) and most of them contained high relative
430 fungal dark diversity, while the bottom half of the plots, those having the lowest amplitude and
431 dark diversity, were mostly old forests or shrublands with a more well-developed vegetation
432 structure (e.g., dead or fallen wood, or complex sub-canopy layer).

433 In open habitats, amplitude and echo-ratio were negatively and positively related to
434 fungal dark diversity, respectively. These results indicate that fewer species are missing from the
435 more even early-successional grasslands without trees and shrubs. We suggest this could be the
436 result of encroachment due to the widespread abandonment of ancient grassland management
437 practices resulting in a loss of small-statured typical grassland plant species without a
438 corresponding gain in species associated with scrub and woodland. It could also reflect that
439 fewer species are missing from calcareous or sandy grasslands since open limestone and white
440 sand have a relatively high reflectivity.

441 ***Plant richness***

442 The most important field-measured variable for modelling fungal dark diversity was plant
443 species richness which was negatively related to dark diversity in both open habitats and
444 woodlands. Plant richness and composition are well-known to correlate with fungal richness and
445 composition (Zak *et al.* 2003, Chen *et al.* 2017, Yang *et al.* 2017, Brunbjerg *et al.* 2018, Wang *et*
446 *al.* 2018), and sites with lower plant species richness have previously been found to have a
447 relatively higher proportion of plants in the dark diversity (Fløjgaard *et al.* 2020). Here, the
448 negative relation between plant richness and fungal dark diversity may be attributed to greater
449 plant richness frequently associated with more stable communities and ecosystems (Kuiters
450 2013, Pellkofer *et al.* 2016, Yang *et al.* 2018), which could indicate longer continuity and hence
451 time for fungi to establish. Alternatively, host specific fungi species could be missing due to
452 absence of their symbiotic plant species (Dickie 2007). However, in our study, plant richness had
453 almost the same effect on both fungal dark diversity accounting for present plant species and
454 where these presences were unaccounted for. This points to plant hosts playing a minor role for
455 fungal dark diversity, which is unsurprising as it likely indicates that the calculation of fungal

456 dark diversity using the Beals' index does not allow fungi having non-present hosts into the site-
457 specific species pool. Another possible explanation is that plant richness mirrors human impact.
458 Generally plant species richness have declined over several decades and continue to as a
459 consequence of agricultural intensification and abandonment of extensive land-use (Hülber *et al.*
460 2017). Other studies have found human disturbance to be strongly related to fungal richness and
461 dark diversity patterns (Epp Schmidt *et al.* 2017, Pärtel *et al.* 2017a), and future studies may help
462 to tease apart these effects.

463 ***Abiotic environment***

464 Soil fertility is often associated with fungal diversity (Balsler *et al.* 2005, Kalliokoski *et*
465 *al.* 2010, Sterkenburg *et al.* 2015) and was found to have a positive relationship with dark
466 diversity in open habitats. In general, soil fertility influences plant species richness negatively
467 through asymmetric competition (Buckland and Grime 2000, Dybzinski *et al.* 2008, Nadeau and
468 Sullivan 2015, Luo *et al.* 2017). This could explain the negative relationship between the local
469 dark diversity of fungi and soil fertility: lower plant species richness yields a higher dark
470 diversity (see discussion above on "Plant richness"). However, the effect might also be
471 uncoupled from plants and simply due to changes in the soil decomposition microbiota from
472 fungal to bacterial dominance along a gradient of soil fertility and pH (Blagodatskaya and
473 Anderson 1998). Another alternative explanation is that soil fertility affects the density of soil
474 mycophagous and microarthropod species (Cole *et al.* 2005) which also may affect fungal dark
475 diversity (Crowther *et al.* 2013). However, while this explanation might be plausible, the
476 underlying mechanisms are largely unknown, calling for further research to dissect the
477 interactions between soil fertility, soil microarthropods and fungal diversity.

478 We also found soil moisture had a positive relationship with fungal dark diversity in open
479 habitats. Moisture is known to influence fungal communities (Gómez-Hernández and Williams-
480 Linera 2011, Gupta *et al.* 2018, Frøslev *et al.* 2019) as it affects the growth, colonization rate,
481 and spore and fruit body production (Salusso and Moraña 1995, Jacobson 1997, Kennedy and
482 Peay 2007). The relationship between fungi and plants is probably important in this regard
483 because soil moisture causes a high turnover in plant species composition (e.g., Moeslund *et al.*
484 (2013), and in turn, affects the quality and availability of resources for below-ground fungal
485 communities (Chen *et al.* 2017). Additionally, high soil moisture is a strong environmental filter

486 excluding most macro-fungi species from the wet habitats (Heilmann-Clausen *et al.* 2019). This
487 filter may also be the main reason for the higher fungal dark diversity found in the wet habitats
488 when plant co-occurrences was not included in determining the site-specific species pool. On the
489 other hand, the interdependencies between fungi and plants, and the strong link between plant
490 communities and soil moisture gradients (Xiong *et al.* 2003, Silvertown *et al.* 2015, Valdez *et al.*
491 2019), may explain why soil moisture was not significant in models where plant co-occurrences
492 was included in determining the site-specific species pool, as this approach perhaps accounts for
493 these interactions.

494 **Uncertainties**

495 One drawback of basing a study on an organism group like fungi, which live a mostly
496 hidden life, is the unavoidable issues concerning overlooked species and hidden diversity in
497 general (Milberg *et al.* 2008, Abrego *et al.* 2016). If such errors are biased towards specific plots
498 our results could be affected. However, the field-work behind the dataset used here was planned
499 to avoid this exact issue by including several visits at each site at different times of the year, and
500 we do not believe this confounds our findings. Nevertheless, there is always uncertainty when
501 estimating unknowns, such as which species are actually absent despite the fact that they could
502 indeed be in a given site. In this study we used on of the most comprehensive and best possible
503 data set along with state-of-the-art methods to calculate these estimates (see e.g. (Lewis *et al.*
504 2016, Moeslund *et al.* 2017), and we therefore believe our results are indeed sound and realistic
505 despite this uncertainty.

506 **Conclusion**

507 This is the first study to investigate potential drivers of the local dark diversity of fungi
508 using both LiDAR derived vegetation and terrain structure as well as field-measured variables.
509 We showed that local fungal dark diversity is strongly dependent on the environment with
510 vegetation structure, plant diversity, and abiotic factors playing important roles. Also, to our
511 knowledge, this is the first study using cross-species group co-occurrence data to determine
512 species pools. This may be a more ecologically sound methodology than using only one taxon
513 group, especially for interdependent taxonomic groups. Future studies and novel approaches will
514 be required to unravel the causal links between fungal communities and habitat and vegetation
515 characteristics; and to gain a better understanding of how LIDAR-based measures can be

516 interpreted as measures of vegetation and terrain structure. Using LiDAR as a tool to determine
517 dark diversity, in conjunction with ecological field measurements, may provide a valuable tool to
518 better guide conservation and restoration planning by identifying sites with high restoration
519 potential (high dark diversity) and high priority for conservation (low dark diversity, or sites
520 where the fungal communities are more “complete”).

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