Investigating the drivers of macro-fungal dark diversity using LiDAR

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Abstract

Despite the important role of fungi for ecosystems, relatively little is known about the factors underlying the dynamics of their diversity. Moreover, studies do not typically consider their dark diversity: the absent species from an otherwise suitable site. Here, we examined the drivers of local fungal dark diversity in temperate woodland and open habitats using LiDAR and in-situ field measurements, combined with a systematically collected and geographically comprehensive (national) macro-fungi and plant data set. For the first time, we also estimated species pools of fungi by considering both plant and fungi co-occurrences. The most important LiDAR variables were amplitude and echo ratio, which are both thought to represent vegetation structure. These results suggest that the local fungal dark diversity is highest in tall dense forests like plantations and lowest in more open forests and open habitats with little woody vegetation. Plant species richness was the most important driver and negatively correlated with local fungal dark diversity. Soil fertility showed a positive relationship with dark diversity in open habitats. This may indicate that the local dark diversity of macro-fungi is highest in areas with a relatively high human impact (typically areas with low plant species richness and high soil fertility). Overall, this study brings novel insights into local macro-fungi dark diversity patterns, suggesting that a

multitude of drivers related to both soil and vegetation act in concert to determine fungal dark diversity. Our results suggest that policymakers and conservation managers should consider plant species richness, soil fertility, and vegetation structure in future management plans for fungal communities.

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

Introduction

Understanding the underlying drivers shaping biodiversity patterns is a central goal in ecology and conservation biology. This is also true for fungi which play a vital role in ecosystem functioning as decomposers, mutualists, and pathogens. However, fungi and the underlying environmental factors influencing fungal diversity is less studied than animals and plants, and quantifying fungal diversity is far from trivial. The most commonly used biodiversity metric is observed species richness (Mueller 2011). However, this measure is not always suitable for comparisons across habitats and conveys no information on the part of the diversity that is potentially missing in a given site (Pärtel et al. 2011). In addition, monitoring fungal diversity is often severely hampered by detectability issues and the life history of the involved species (Blackwell and Vega 2018; Yahr et al. 2016). Several alternative approaches have been developed to more effectively monitor and compare biodiversity across landscapes (Ricotta 2005, 2007; Sarkar and Margules 2002; Solow and Polasky 1994). Although these methods can provide valuable insights, they do not consider the dark diversity, the absent part of the species pool which can potentially inhabit an environmentally suitable site (Pärtel et al. 2011). This often-ignored aspect of diversity provides a novel and ecologically meaningful metric for estimating how much of the potential species diversity – the site specific species pool – is lacking (Pärtel et al. 2011). This information is important in both studies of community assembly, and its underlying mechanisms and dynamics, but also for conservation and restoration management (Lewis et al. 2017; Mateo et al. 2017). Here, we use fungal data from 130 thoroughly inventoried sites covering all terrestrial habitats, from open to forest, and wet to arid, to investigate important drivers of fungal dark diversity.

Dark diversity aims to reconcile the role of simultaneous, and potentially confounding, regional and local processes underlying biodiversity patterns and biological communities (Pärtel

2014; Pärtel et al. 2011). In any given landscape, the biodiversity potential is ultimately determined by large-scale biogeographic and evolutionary processes (i.e., species diversification and historic migration patterns) which create the set of species which can theoretically inhabit a site, defined as the species pool (Cornell and Harrison 2014; Pärtel et al. 1996; Zobel 2016). This species pool is further filtered by local processes such as environmental gradients, species interactions, population dynamics, dispersal, disturbance, and stochastic events (Cornell and Harrison 2014; Pärtel et al. 2013; Ronk et al. 2015; Zobel 2016). Only a few studies have focused on the determinants of fungal dark diversity. These studies demonstrate that higher temperatures increases arbuscular mycorrhizal dark diversity (Pärtel et al. 2017a) and annual precipitation decreases the dark diversity of ectomycorrhizal fungi at the global scale (Pärtel et al. 2017b). These results concur with previous research suggesting large scale climatic factors are strong drivers of fungal richness and community composition, attributed to the direct and indirect effects which alter soil and floristic conditions (Kivlin et al. 2011; Staddon et al. 2003; Tedersoo et al. 2014). Local edaphic conditions such as soil moisture, pH, and calcium concentration are also known to influence fungal diversity (Frøslev et al. 2019; Geml et al. 2014; Tedersoo et al. 2014; Tonn and Ibáñez 2017), but the effects of these conditions on dark diversity still remain unknown.

Besides the influence of environmental gradients, other factors particularly important for fungi are vegetation and habitat structure, such as vegetation height, shrub layer, vegetation cover, dead wood, and other woody features (Gómez-Hernández and Williams-Linera 2011; Humphrey et al. 2000; Nordén and Paltto 2001; Nordén et al. 2004; Zuo et al. 2016). As the dominant primary producer in terrestrial ecosystems, plants also form the living and dead organic carbon pools and biotic surfaces that are the niche space for not only fungi but other taxonomic groups as well (Brunbjerg et al. 2017; DeAngelis 2012). The importance of these structural elements has recently been found to influence the diversity of not only fungi, but plants, animals, and bacteria as well (Penone et al. 2019). Despite the obvious contribution of these variables, such factors are rarely covered extensively since they are difficult to measure and require large amounts of resources to obtain sufficient and high-quality data. However, emerging technologies such as LiDAR (light detection and ranging) could potentially remedy this situation.

Airborne LiDAR records a three-dimensional set of points using laser ranging from an aircraft or a drone (Lefsky et al. 2002). It captures data suitable to represent many of the vegetation and landscape structural measures important to fungi (Lopatin et al. 2016; Mao et al. 2018; Peura et al. 2016; Thers et al. 2017; Vehmas et al. 2009). As a relatively new methodology, biodiversity studies that employ LiDAR have been limited in scope, typically addressing only one taxonomic group or habitat type at the local scale, and strongly biased towards forest ecosystems. However, studies using LiDAR-based indicators have already been shown to explain up to 66% and 82% of local plant and fungi richness, respectively (Lopatin et al. 2016; Peura et al. 2016; Thers et al. 2017). A recent study has demonstrated its potential to provide spatially accurate and comprehensive measures by predicting the local biodiversity of different taxonomic groups (plants, fungi, lichens, and bryophytes) across multiple habitat types and large geographic extent (Moeslund et al. 2019). LiDAR may also be a useful tool in studying dark diversity by incorporating potentially important spatiotemporal dynamics such as succession and disturbance (Mokany and Shine 2003; Pärtel et al. 2013; Scott et al. 2011). Previous studies have hinted at the effect of these processes on dark diversity increase dark diversity in arbuscular mycorrhizal fungi (Pärtel et al. 2017a), ruderal plants are more likely to be in dark diversity (Moeslund et al. 2017), and human density and agricultural land use influence dark diversity of vascular plants (Riibak et al. 2017). However, factors such as succession have been actively excluded to avoid complications in quantifying dark diversity where species are not in equilibrium with environmental conditions (Pärtel et al. 2017a).

Alongside these structural and environmental factors, fungal diversity depends on biotic interactions, with a large proportion of fungi deriving their nutrients and carbon from host plants. These biotrophic fungi consist mainly of mycorrhizal fungi which form a mutualistic relationship with living roots of a plant, and pathotrophic fungi that receive nutrients by harming or killing host plants (Nguyen et al. 2016; Tedersoo et al. 2014). Recent evidence has hinted on the influence of these trophic interactions, as plant species dependent on mycorrhiza have been found to have greater dark diversity than those without these mutualist relationships (Moeslund et al. 2017). A recent study indicates that ectomycorrhizal fungal diversity increased exponentially with an increasing proportion of their host plants, suggesting that competitive interactions among fungi with a high abundance of hosts might also drive their dark diversity (Pärtel et al. 2017b). Typically, inter-specific interactions are indeed considered in methods for

estimating dark diversity as these are usually based on species co-occurrence patterns also assuming that co-occurrence is a proxy for shared abiotic requirements and biogeographical history (Beals 1984; de Bello et al. 2012; Lewis et al. 2016; McCune 1994; Münzbergová and Herben 2004). However, this is usually done while considering only species within the species group being studied. Recognizing the close and interconnected relationship between plants and fungi allows for stronger and more realistic estimations of the fungal dark diversity. Incorporating other taxonomic groups when determining species pools and estimating dark diversity is not a new insight, and the importance of other biotic interactions across trophic groups has been discussed since the concept of dark diversity was first introduced (Pärtel et al. 2011). However, it is yet to be done, and the exclusion of non-competitive biotic interactions means that there is a large component missing in describing dark diversity, and may explain why dark diversity is sometimes over-estimated (Boussarie et al. 2018).

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

Methods

Study area and site selection

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

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

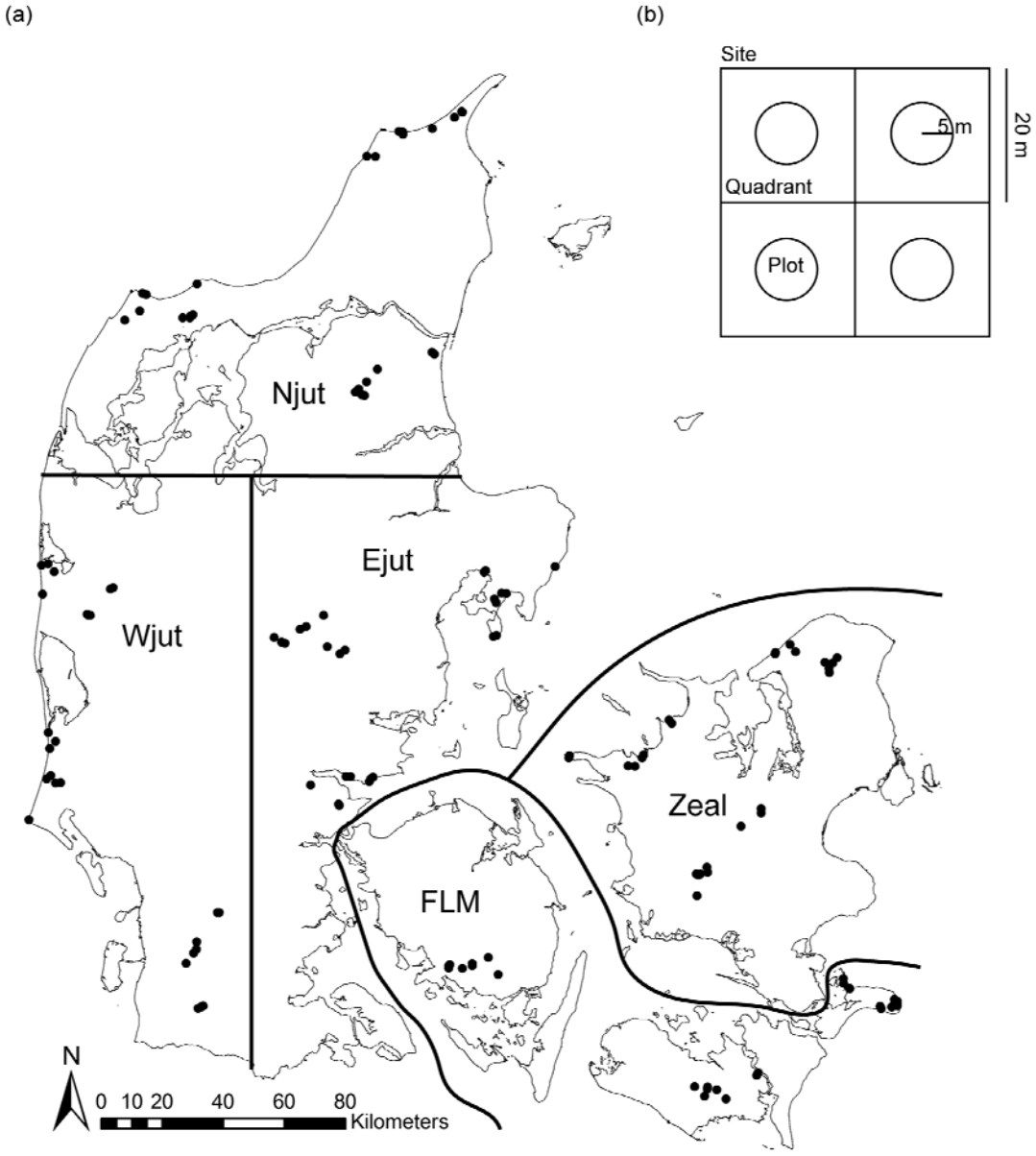

Figure 1. The 130 selected study sites from a national biodiversity inventory. Reprinted from Ejrnæs et al. (2018), with permission from Elsevier.

Field-measured variables

We used fungi observational data from the "Biowide" field inventories. Macro-fungal species were surveyed in 2014–2015 by expert field-mycologists during three inventories (up to one hour per site) in the main fruiting season (August - November) by actively searching microhabitats and substrates (soil, herbaceous vegetation and debris, dead wood, litter, and bark

of trees up to 2 m) within the 40 × 40 m sites. Since truffles are difficult to find, we did not consider these in this study. Vascular plant species observations were also taken from the "Biowide" database and were originally inventoried by trained botanists during the summer 2014 and spring 2015 to account for variations in phenology. We removed all subspecies, hybrids, variations, and neophytes (i.e. species that are not considered a natural part of the vegetation given their history and dispersal ability, see appendix tables 6–8 in Buchwald et al. (2013)). Species nomenclature follow the species checklist of Denmark (allearter.dk).

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

177 Table 1. Overview of the explanatory variables for fungal dark diversity models along with our hypothesized relationship with dark
178 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	Plant richness increases community stability or reflect low human impact. This would result in more available hosts and therefore a lower dark diversity	(Kuiters 2013; Pellkofer et al. 2016; Yang et al. 2018)
	Organic matter as carbon resources -litter (open habitats) -dead wood (forests)	Organic matter increases competition between fungi and soil bacteria which would increase dark diversity. Alternatively, the more substrate represented by more organic matter gives more resources for fungi and hence a lower dark diversity	(Averill et al. 2014; Leigh et al. 2011)
	Soil pH	Soil pH increases fungal richness and colonization, and reduces competition with soil microbes, lowering dark diversity	(Clark 1997; Rousk et al. 2010; Rousk et al. 2009)
	Soil fertility index (SFI)	Soil fertility increases fungal and host plant competitiveness and often reflects a higher human impact, which would probably increase dark diversity	(Buckland and Grime 2000; Liu et al. 2015; Luo et al. 2017; Nadeau and Sullivan 2015)
	Soil moisture index (SMI)	Soil moisture increases fungal growth,	(Jacobson 1997; Kennedy and

		colonization rate, and spore production, increasing dark diversity. Alternatively, the relationship could be unimodal, with high dark diversity at intermediate-high moisture levels	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 niches for potential fungal species increasing their dark diversity	(Gómez et al. 2019; Zuo et al. 2016)
	Succession (Amplitude)	Amplitude could reflect successional processes with later successional stages allowing fungi to become more established, resulting in lower dark diversity	(Fernández-Toirán et al. 2006; Hui et al. 2017; Twieg et al. 2007)
	Microtopography -Terrain roughness (SigmaZ) -Terrain openness*	Microtopography increases availability of niches and increases dark diversity	(Cantelmo Jr and Ehrenfeld 1999)
	Light/heat - Canopy openness (forests)* -Heat load index* -Solar irradiation* -Vegetation cover*	Light increases fungal colonization which would decrease dark diversity	(Graham et al. 1982; Turner et al. 2009)

Canopy complexity -Echo ratio*	Canopy complexity provides more niches increasing potential fungal diversity and dark diversity	(Dove and Keeton 2015; Gómez-Hernández and Williams-Linera 2011; Unterseher and Tal 2006)

LiDAR-based measures

To enable the calculation of measures representing vegetation and terrain environmental and structural aspects, we used the latest nationally covering LiDAR-based point cloud for Denmark from the Danish Ministry of Environment. This dataset is freely available from www.kortforsyningen.dk and has a point density of 4-5 points/m^2. Originally, this dataset was recorded from fixed-wing airplanes at an altitude of approximately 680 m above ground level and a speed over ground of approximately 240 km/h. The data was recorded by Riegl LMS-680i scanners operating in the near-infrared wavelength (1550 nm) in a parallel line scan pattern during the springs and autumns of 2014 and 2015. For all calculations, we relied on the classification of points into ground, building and vegetation classes already present in the data set upon download.

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

Vegetation-related measures

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

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

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

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

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

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

Terrain-structure measures

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

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

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

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

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

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

Data analysis

Data preparation

Prior to statistical analysis, we removed the six intensively managed fields from the study sites, as these are ploughed fields with no nature value. We also removed two study sites because they were flooded during the LiDAR data recording period. Finally, we removed one site due to

266 an extreme outlier in the LiDAR amplitude values (300 vs. a range of values between 10 and
267 130). Our final dataset therefore comprised a total of 121 study sites.

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

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

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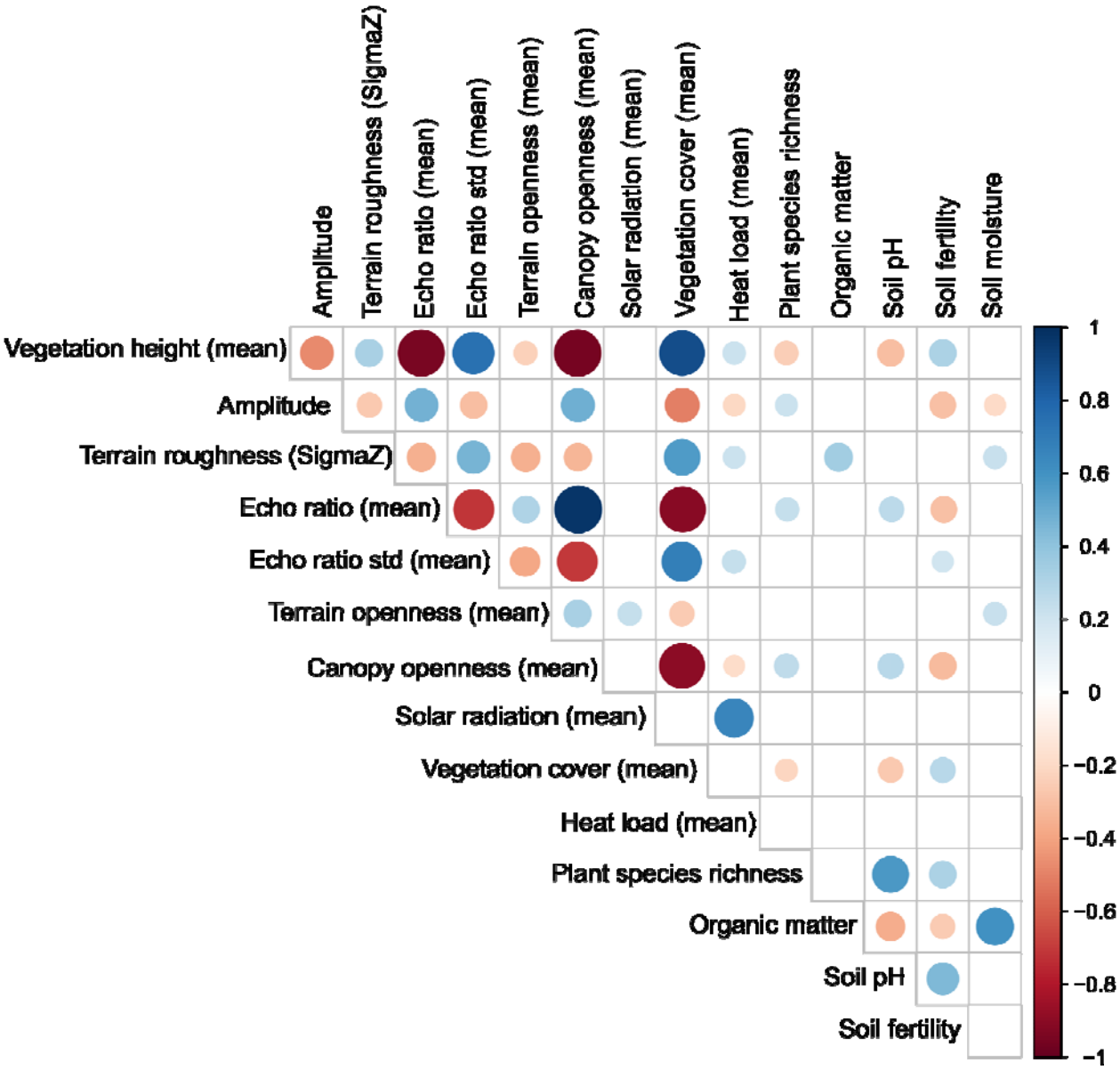
Appendix 1. Correlation plot between environmental and LiDAR variables. All significant interactions are colored red for negative relationships and blue for positive relationships, with the size and darkness of the color representing the strength of the relationship. Non-significant correlations are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



Dark diversity

All statistical analyses mentioned in the following were performed in R version 3.5.3 (R Core Team 2019). To determine fungal dark diversity estimates based on co-occurrence with plants (see below), we only used records of fungal species recorded where they had at least one

co-occurrence with a plant genus. This restriction was based on the database from the Danish Fungi Atlas project (svampeatlas.dk), containing over 150,000 fungal records (available through gbif.org) and plant co-occurrence data for 2,006 fungal species. We calculated the regional pool using the Beals' index (Beals 1984), as recommended by Lewis et al. (2016), using the 'beals' function in the 'vegan' package (Oksanen et al. 2017). The Beals' index represents the probability that a particular species will occur within a given site based on the assemblage of co-occurring species (Beals 1984; McCune 1994; Münzbergová and Herben 2004). The threshold used for including a particular species in the regional species pool was the 5^{th} percentile of the Beals' index value for each species (Gijbels et al. 2012; Ronk et al. 2015). Preceding the calculation of each threshold, the lowest Beals' index value among plots with the occurrence of the species in question was identified, and all plots having values below the minimum were not considered. We calculated two measures of the regional pool for each site: (1) using only fungi co-occurrence and (2) co-occurrences of both observed fungi and vascular plants at each site to acknowledge the fungal-plant linkages. Dark diversity was calculated by subtracting observed fungal species richness from the regional pool. Since site-specific species pools differ between sites, we calculated the relative dark diversity for each site as dark diversity (species predicted from the regional pool but not observed) divided by the regional pool to enable comparison of results across habitats.

Statistical analysis

To investigate what characterizes sites with a high fungal dark diversity we constructed GLMs with a Gaussian link having the estimated relative dark diversity as the response variable. We constructed models for both open habitats and woodlands, and for both dark diversity estimates (see the section on dark diversity). Initially, we fitted models using only the LiDAR measures as explanatory factors, to test the degree to which fungal dark diversity patterns could be explained using LiDAR data alone. Subsequently, we fitted a similar model with both measured and LiDAR variables as explanatory factors (Table 1), giving insight into how much more explanatory power one gains by using measured variables in addition to LiDAR. To allow for non-linear relationships for variables corresponding to the intermediate disturbance hypothesis (Connell 1978; Townsend et al. 1997) and intermediate productivity hypothesis (Fraser et al. 2015), we used Akaike's Information Criterion (AIC) (Burnham and Anderson

2002) to evaluate if inclusion of squared terms for the variables SMI, SFI, light, soil pH, and bare soil (see Table 1) improved the model fit. If so, we kept the squared term of the variable in question instead of the linear effect. After the initial fit and checking for non-linearity as described above, we ran a backward model selection procedure for each model based on AIC. The procedure stopped when AIC did not drop anymore and ΔAIC was above 2 (Burnham and Anderson 2002). In each iteration, we dropped the variable causing the smallest change in AIC value. As a final step, we checked model residuals to ensure that these were normally distributed.

Results

In most cases, our models explained between 20-30 % of the variation in fungal dark diversity and more than 40 % for the woodlands models when including both LiDAR and measured variables (Table 2). The only LiDAR variable significant in both open habitats and woodlands was amplitude, which was significant in all models for woodlands and in LiDAR-only models for open habitats (Table 2). This variable had a positive effect on dark diversity in woodlands (Table 2) but a negative influence in open habitats (Table 2). Echo ratio was the only other significant LiDAR variable in our analyses and positively influenced dark diversity in open habitats (Table 2). Plant richness was negatively related to local fungal dark diversity and had the strongest impact of all the field-measured factors included in our analyses (Table 2). Also, soil fertility and moisture were positively correlated with fungal dark diversity in open habitats (Table 2). In all cases, models considering only the structural environment (LiDAR only) were outperformed by models considering plant richness and the abiotic environment in addition to the structural, notably in the open habitats (Table 2). Appendix 1 shows all pair-wise Spearman correlations between the explanatory variables used.

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

Discussion

In this study, we demonstrate for the first time that LiDAR derived variables, alone and in combination with field-measured variables, can explain a significant amount of the variation in local dark diversity of temperate macro-fungal communities. Our findings indicate that the dark diversity of fungi, is influenced by habitat characteristics such as the local vegetation structure, plant associations, and the abiotic environment. This is not surprising since local observed fungal diversity is also determined by these factors to a large degree (Moeslund et al. 2019; Thers et al. 2017; Yang et al. 2017). We also find that models including field-based variables explained the dark diversity of fungi far better than models relying solely on LiDAR, notably in open landscapes. While LiDAR has the advantage that one can record data from huge areas in very fine detail for relatively low cost, our results indicates that to get the best explanation of local fungal diversity patterns fieldwork is still needed. Nevertheless, these findings emphasize the importance of focusing on habitat characteristics in the restoration and conservation of fungal communities, notably those where specific species are apparently missing judged from the community composition.

LiDAR-based measures

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

The LiDAR measure of amplitude is sensitive both to surface reflectivity and to the number of targets hit by the laser pulse (Moeslund et al. 2019). The lower the reflectivity and the more targets between which the light energy is distributed, the lower the amplitude associated with a given point. This would result in high amplitudes in flatter surfaces while yielding low amplitudes in tall and more open complex canopies, or translucent surfaces such as leaves. Hence, this variable can be a proxy for succession, surface evenness, or vegetation density; since

both flat and sparsely vegetated as well as densely vegetated canopies preventing light penetration will yield high amplitude. Supporting this, amplitude was positively correlated with vegetation height and vegetation cover (denser vegetation resulted in higher amplitude) and negatively correlated with echo ratio (vegetation complexity, see below) and canopy openness. In woodlands, the dark diversity of fungi was positively related to amplitude, suggesting that more species are missing in the relatively tall and dense forests compared to more complex and open woodlands. The positive association between LiDAR amplitude and dark diversity could therefore be a consequence of communities in older well-developed shrubland or old-growth pristine forests with windthrows or other openings, having allowed fungi more time to become established with their associated plants (Fernández-Toirán et al. 2006; Twieg et al. 2007). Indeed, among the top half of woodland plots with regards to amplitude were plantations and most of them contained rather high relative fungal dark diversity, while the bottom half of the plots, those having the lowest dark diversity, were mostly old forests or shrublands with a well-developed vegetation structure (e.g., dead or fallen wood or complex sub-canopy layer).

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

Plant richness

The most important field-measured variable was plant species richness which was negatively related to fungal dark diversity in both open habitats and woodlands. Plant richness and composition are well-known to correlate with fungal richness and composition (Brunbjerg et al. 2018; Chen et al. 2017; Wang et al. 2018; Yang et al. 2017; Zak et al. 2003), and sites with lower plant species richness have previously been found to have a relatively higher proportion of plants in the dark diversity (Fløjgaard et al. 2020). These results may be attributed to greater plant richness associated with more stable communities and ecosystems (Kuiters 2013; Pellkofer

et al. 2016; Yang et al. 2018), which could indicate longer continuity and hence time for fungi to establish. Alternatively, host specific fungi species could be missing due to absence of their symbiotic plant species (Dickie 2007). In that case, a higher plant species richness could mean the presence of more symbiont plant species and therefore more fungi can establish at sites where suitable symbionts are more plentiful. Another possible explanation is that plant richness mirrors human impact. Generally plant species richness have declined over several decades and continue to as a consequence of agricultural intensification and abandonment of extensive land-use (Hülber et al. 2017). Other studies have found human disturbance to be a strong driver of fungal richness and dark diversity patterns (Epp Schmidt et al. 2017; Pärtel et al. 2017a), and future studies may help to tease apart these effects.

Abiotic environment

Soil fertility is an important driver of fungal communities (Balser et al. 2005; Kalliokoski et al. 2010; Sterkenburg et al. 2015) and was found to have a positive relationship with dark diversity in open habitats. In general, soil fertility influences plant species richness negatively through asymmetric competition (Buckland and Grime 2000; Dybzinski et al. 2008; Luo et al. 2017; Nadeau and Sullivan 2015). This likely explains the negative relationship between the local dark diversity of fungi and soil fertility: lower plant species richness possibly resulting in a lower number of suitable hosts for host-specific fungal species. However, the effect might also be uncoupled from plants and simply due to changes in the soil decomposition microbiota from fungal to bacterial dominance along a gradient of soil fertility and pH (Blagodatskaya and Anderson 1998). Another alternative explanation is that soil fertility affects the density of soil mycophagous and microarthropod species (Cole et al. 2005) which also affects fungal dark diversity (Crowther et al. 2013). However, while this explanation might be plausible, the underlying mechanisms are largely unknown, calling for further research to dissect the interactions between soil fertility, soil microarthropods and fungal diversity.

We also found soil moisture had a positive relationship with fungal dark diversity in open habitats. Moisture is an important driver of fungal communities (Frøslev et al. 2019; Gómez-Hernández and Williams-Linera 2011; Gupta et al. 2018) and the availability of water increases the growth, colonization rate, and spore production of fungi (Jacobson 1997; Kennedy and Peay 2007). The relationship between fungi and plants is also important because moisture plays a key

role in regulating ecosystem functioning which affects the primary production of the aboveground plant communities (Bai et al. 2004), and in turn the quality and availability of resources for below-ground fungal communities (Chen et al. 2017). High soil moisture is a strong environmental filter excluding most macro-fungi species in the wet habitats (e.g., 29 of the Danish red-listed fungal species are from wetlands, whereas 441 species are from grasslands and forests). This filter may also be the main reason for the higher fungal dark diversity found in the wet habitats. The interdependencies between fungi and plants, and the strong link between plant communities and soil moisture gradients (Silvertown et al. 2015; Valdez et al. 2019; Xiong et al. 2003), may explain why moisture was not significant in models of fungal dark diversity based on both plant and fungal co-occurrences, as this approach perhaps accounts for these interactions.

Conclusion

This is the first study to investigate the drivers of the local dark diversity of fungi using both LiDAR derived vegetation and terrain structure as well as field-measured variables. We showed that local fungal dark diversity is strongly dependent on the environment with vegetation structure, plant diversity, and abiotic factors playing important roles in determining fungal dark diversity. Also, to our knowledge, this is the first study determining regional pools with species co-occurrence across taxon groups. This may be a much more ecologically sound methodology than using only one taxon group, especially for interdependent taxonomic groups. Future studies and novel approaches will be required to disentangle the various effects of LiDAR and field-measured variables on dark diversity, especially since LiDAR variables are proxies for what we wish to measure. Using LiDAR as a tool to determine dark diversity, in conjunction with ecological field measurements, may be a valuable tool to better guide conservation and restoration planning by identifying sites having a high dark diversity.

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Literature Cited

Averill, C., Turner, B.L., & Finzi, A.C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature, 505*, 543-545

Bai, Y., Han, X., Wu, J., Chen, Z., & Li, L. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature, 431*, 181-184

Balser, T.C., Treseder, K.K., & Ekenler, M. (2005). Using lipid analysis and hyphal length to quantify AM and saprotrophic fungal abundance along a soil chronosequence. *Soil Biology and Biochemistry, 37*, 601-604

Beals, E.W. (1984). Bray-Curtis ordination: An effective strategy for analysis of multivariate ecological data. In A. MacFadyen, & E.D. Ford (Eds.), *Advances in Ecological Research* (pp. 1-55): Academic Press

Blackwell, M., & Vega, F.E. (2018). Lives within lives: Hidden fungal biodiversity and the importance of conservation. *Fungal Ecology, 35*, 127-134

Blagodatskaya, E.V., & Anderson, T.-H. (1998). Interactive effects of pH and substrate quality on the fungal-to-bacterial ratio and qCO2 of microbial communities in forest soils. *Soil Biology and Biochemistry, 30*, 1269-1274

Boussarie, G., Bakker, J., Wangensteen, O.S., Mariani, S., Bonnin, L., Juhel, J.-B., Kiszka, J.J., Kulbicki, M., Manel, S., & Robbins, W.D. (2018). Environmental DNA illuminates the dark diversity of sharks. *Science advances, 4*, eaap9661

Brunbjerg, A.K., Bruun, H.H., Broendum, L., Classen, A.T., Fog, K., Froeslev, T.G., Goldberg, I., Hansen, M.D.D., Hoeye, T.T., Laessoee, T., Newman, G., Skipper, L., Soechting, U., &

Ejrnaes, R. (2019). A systematic survey of regional multitaxon biodiversity: evaluating strategies and coverage. *BMC Ecology, 19,* 158030

Brunbjerg, A.K., Bruun, H.H., Dalby, L., Fløjgaard, C., Frøslev, T.G., Høye, T.T., Goldberg, I., Læssøe, T., Hansen, M.D., & Brøndum, L. (2018). Vascular plant species richness and bioindication predict multi□taxon species richness. *Methods in Ecology and Evolution, 9,* 2372-2382

Brunbjerg, A.K., Bruun, H.H., Moeslund, J.E., Sadler, J.P., Svenning, J.-C., & Ejrnæs, R. (2017). Ecospace: A unified framework for understanding variation in terrestrial biodiversity. *Basic and Applied Ecology, 18,* 86-94

Buchwald, E., Wind, P., Bruun, H.H., Møller, P.F., Ejrnæs, R., & Svart, H.E. (2013). Hvilke planter er hjemmehørende i Danmark? *Flora & Fauna, 118,* 73-96

Buckland, S.M., & Grime, J.P. (2000). The effects of trophic structure and soil fertility on the assembly of plant communities: a microcosm experiment. *Oikos, 91,* 336-352

Burnham, K.P., & Anderson, D.R. (2002). *Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach*. New York: Springer

Cantelmo Jr, A.J., & Ehrenfeld, J.G. (1999). Effects of microtopography on mycorrhizal infection in Atlantic white cedar (Chamaecyparis thyoides (L.) Mills.). *Mycorrhiza, 8,* 175-180

Chen, Y.-L., Xu, T.-L., Veresoglou, S.D., Hu, H.-W., Hao, Z.-P., Hu, Y.-J., Liu, L., Deng, Y., Rillig, M.C., & Chen, B.-D. (2017). Plant diversity represents the prevalent determinant of soil fungal community structure across temperate grasslands in northern China. *Soil Biology and Biochemistry, 110,* 12-21

Clark, R.B. (1997). Arbuscular mycorrhizal adaptation, spore germination, root colonization, and host plant growth and mineral acquisition at low pH. *Plant and Soil, 192,* 15-22

520 Cole, L., Buckland, S.M., & Bardgett, R.D. (2005). Relating microarthropod community
521 structure and diversity to soil fertility manipulations in temperate grassland. *Soil Biology and*
522 *Biochemistry, 37*, 1707-1717
523 Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science, 199*, 1302-1310
524 Cornell, H.V., & Harrison, S.P. (2014). What are species pools and when are they important?
525 *Annual Review of Ecology, Evolution, and Systematics, 45*, 45-67
526 Crowther, T.W., Stanton, D.W., Thomas, S.M., A'Bear, A.D., Hiscox, J., Jones, T.H., Voříšková,
527 J., Baldrian, P., & Boddy, L. (2013). Top□down control of soil fungal community composition
528 by a globally distributed keystone consumer. *Ecology, 94*, 2518-2528
529 de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P.,
530 Götzenberger, L., Lavergne, S., & Lepš, J. (2012). Functional species pool framework to test for
531 biotic effects on community assembly. *Ecology, 93*, 2263-2273
532 DeAngelis, D.L. (2012). *Dynamics of nutrient cycling and food webs*. Springer Science &
533 Business Media
534 Dickie, I.A. (2007). Host preference, niches and fungal diversity. *The New Phytologist, 174*, 230-
535 233
536 Doneus, M. (2013). Openness as visualization technique for interpretative mapping of airborne
537 lidar derived digital terrain models. *Remote Sensing, 5*, 6427-6442
538 Dove, N.C., & Keeton, W.S. (2015). Structural Complexity Enhancement increases fungal
539 species richness in northern hardwood forests. *Fungal Ecology, 13*, 181-192
540 Dybzinski, R., Fargione, J.E., Zak, D.R., Fornara, D., & Tilman, D. (2008). Soil fertility
541 increases with plant species diversity in a long-term biodiversity experiment. *Oecologia, 158*,
542 85-93

543 Ejrnæs, R., Frøslev, T.G., Høye, T.T., Kjøller, R., Oddershede, A., Brunbjerg, A.K., Hansen,
544 A.J., & Bruun, H.H. (2018). Uniquity: A general metric for biotic uniqueness of sites. *Biological*
545 *Conservation*, *225*, 98-105
546 Epp Schmidt, D.J., Pouyat, R., Szlavecz, K., Setälä, H., Kotze, D.J., Yesilonis, I., Cilliers, S.,
547 Hornung, E., Dombos, M., & Yarwood, S.A. (2017). Urbanization erodes ectomycorrhizal
548 fungal diversity and may cause microbial communities to converge. *Nature ecology & evolution*,
549 *1*, 0123
550 Fernández-Toirán, L.M., Ágreda, T., & Olano, J.M. (2006). Stand age and sampling year effect
551 on the fungal fruit body community in Pinus pinaster forests in central Spain. *Canadian Journal*
552 *of Botany*, *84*, 1249-1258
553 Fløjgaard, C., Valdez, J.W., Dalby, L., Moeslund, J.E., Clausen, K.K., Ejrnæs, R., Pärtel, M., &
554 Brunbjerg, A.K. (2020). Dark diversity reveals importance of biotic resources and competition
555 for plant diversity across broad environmental gradients. *Ecology and Evolution*, *00*, 1– 11
556 Fraser, L.H., Pither, J., Jentsch, A., Sternberg, M., Zobel, M., Askarizadeh, D., Bartha, S.,
557 Beierkuhnlein, C., Bennett, J.A., & Bittel, A. (2015). Worldwide evidence of a unimodal
558 relationship between productivity and plant species richness. *Science*, *349*, 302-305
559 Frøslev, T.G., Kjøller, R., Bruun, H.H., Ejrnæs, R., Hansen, A.J., Læssøe, T., & Heilmann-
560 Clausen, J. (2019). Man against machine: Do fungal fruitbodies and eDNA give similar
561 biodiversity assessments across broad environmental gradients? *Biological Conservation*, *233*,
562 201-212
563 Geml, J., Gravendeel, B., van der Gaag, K.J., Neilen, M., Lammers, Y., Raes, N., Semenova,
564 T.A., de Knijff, P., & Noordeloos, M.E. (2014). The Contribution of DNA Metabarcoding to

565 Fungal Conservation: Diversity Assessment, Habitat Partitioning and Mapping Red-Listed Fungi
566 in Protected Coastal Salix repens Communities in the Netherlands. *PLOS ONE, 9*, e99852
567 Gijbels, P., Adriaens, D., & Honnay, O. (2012). An orchid colonization credit in restored
568 calcareous grasslands. *Écoscience, 19*, 21-28
569 Gómez-Hernández, M., & Williams-Linera, G. (2011). Diversity of macromycetes determined
570 by tree species, vegetation structure, and microenvironment in tropical cloud forests in Veracruz,
571 Mexico. *Botany, 89*, 203-216
572 Gómez, F.J.R., Navarro-Cerrillo, R.M., Pérez-de-Luque, A., Oβwald, W., Vannini, A., &
573 Morales-Rodríguez, C. (2019). Assessment of functional and structural changes of soil fungal
574 and oomycete communities in holm oak declined dehesas through metabarcoding analysis.
575 *Scientific reports, 9*, 5315
576 Graham, J.H., Leonard, R.T., & Menge, J.A. (1982). Interaction of light intensity and soil
577 temperature with phosphorus inhibition of vesicular-arbuscular mycorrhiza formation. *New*
578 *Phytologist, 91*, 683-690
579 Gupta, M.M., Gupta, A., & Kumar, P. (2018). Urbanization and biodiversity of arbuscular
580 mycorrhizal fungi: The case study of Delhi, India. *Revista de Biología Tropical, 66*, 1547-1558
581 Höfle, B., Hollaus, M., & Hagenauer, J. (2012). Urban vegetation detection using radiometrically
582 calibrated small-footprint full-waveform airborne LiDAR data. *ISPRS Journal of*
583 *photogrammetry and remote sensing, 67*, 134-147
584 Höfle, B., & Pfeifer, N. (2007). Correction of laser scanning intensity data: Data and model-
585 driven approaches. *ISPRS Journal of photogrammetry and remote sensing, 62*, 415-433

586 Hui, N., Liu, X., Kotze, D.J., Jumpponen, A., Francini, G., & Setälä, H. (2017). Ectomycorrhizal
587 Fungal Communities in Urban Parks Are Similar to Those in Natural Forests but Shaped by
588 Vegetation and Park Age. *Applied and Environmental Microbiology, 83*, e01797-01717
589 Hülber, K., Moser, D., Sauberer, N., Maas, B., Staudinger, M., Grass, V., Wrbka, T., & Willner,
590 W. (2017). Plant species richness decreased in semi-natural grasslands in the Biosphere Reserve
591 Wienerwald, Austria, over the past two decades, despite agri-environmental measures.
592 *Agriculture, ecosystems & environment, 243*, 10-18
593 Humphrey, J.W., Newton, A.C., Peace, A.J., & Holden, E. (2000). The importance of conifer
594 plantations in northern Britain as a habitat for native fungi. *Biological Conservation, 96*, 241-252
595 Jacobson, K.M. (1997). Moisture and substrate stability determine VA-mycorrhizal fungal
596 community distribution and structure in an arid grassland. *Journal of Arid Environments, 35*, 59-
597 75
598 Junttila, S., Sugano, J., Vastaranta, M., Linnakoski, R., Kaartinen, H., Kukko, A., Holopainen,
599 M., Hyyppä, H., & Hyyppä, J. (2018). Can leaf water content be estimated using multispectral
600 terrestrial laser scanning? A case study with Norway spruce seedlings. *Frontiers in plant science,*
601 *9*, 299
602 Kalliokoski, T., Pennanen, T., Nygren, P., Sievänen, R., & Helmisaari, H.-S. (2010).
603 Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza
604 characteristics along stand developmental stage and soil fertility gradients. *Plant and Soil, 330*,
605 73-89
606 Kennedy, P.G., & Peay, K.G. (2007). Different soil moisture conditions change the outcome of
607 the ectomycorrhizal symbiosis between Rhizopogon species and Pinus muricata. *Plant and Soil,*
608 *291*, 155

609 Kivlin, S.N., Hawkes, C.V., & Treseder, K.K. (2011). Global diversity and distribution of
610 arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry, 43*, 2294-2303
611 Kuiters, A.T. (2013). Diversity–stability relationships in plant communities of contrasting
612 habitats. *Journal of Vegetation Science, 24*, 453-462
613 Kutner, M.H., Nachtsheim, C.J., Neter, J., & Li, W. (2005). *Applied linear statistical models*.
614 McGraw-Hill Irwin Boston
615 Lefsky, M.A., Cohen, W.B., Parker, G.G., & Harding, D.J. (2002). Lidar Remote Sensing for
616 Ecosystem Studies: Lidar, an emerging remote sensing technology that directly measures the
617 three-dimensional distribution of plant canopies, can accurately estimate vegetation structural
618 attributes and should be of particular interest to forest, landscape, and global ecologists.
619 *BioScience, 52*, 19-30
620 Leigh, J., Fitter, A.H., & Hodge, A. (2011). Growth and symbiotic effectiveness of an arbuscular
621 mycorrhizal fungus in organic matter in competition with soil bacteria. *FEMS Microbiology*
622 *Ecology, 76*, 428-438
623 Lewis, R.J., Bello, F., Bennett, J.A., Fibich, P., Finerty, G.E., Götzenberger, L., Hiiesalu, I.,
624 Kasari, L., Lepš, J., Májeková, M., Mudrák, O., Riibak, K., Ronk, A., Rychtecká, T., Vitová, A.,
625 & Pärtel, M. (2017). Applying the dark diversity concept to nature conservation. *Conservation*
626 *Biology, 31*, 40-47
627 Lewis, R.J., Szava□Kovats, R., Pärtel, M., & Evolution (2016). Estimating dark diversity and
628 species pools: an empirical assessment of two methods. *Methods in Ecology, 7*, 104-113
629 Liu, Y., Johnson, N.C., Mao, L., Shi, G., Jiang, S., Ma, X., Du, G., An, L., & Feng, H. (2015).
630 Phylogenetic structure of arbuscular mycorrhizal community shifts in response to increasing soil
631 fertility. *Soil Biology and Biochemistry, 89*, 196-205

632 Lopatin, J., Dolos, K., Hernández, H., Galleguillos, M., & Fassnacht, F. (2016). Comparing
633 generalized linear models and random forest to model vascular plant species richness using
634 LiDAR data in a natural forest in central Chile. *Remote Sensing of Environment, 173*, 200-210
635 Luo, S., De Deyn, G.B., Jiang, B., & Yu, S. (2017). Soil biota suppress positive plant diversity
636 effects on productivity at high but not low soil fertility. *Journal of Ecology, 105*, 1766-1774
637 Mao, L., Dennett, J., Bater, C.W., Tompalski, P., Coops, N.C., Farr, D., Kohler, M., White, B.,
638 Stadt, J.J., & Nielsen, S.E. (2018). Using airborne laser scanning to predict plant species richness
639 and assess conservation threats in the oil sands region of Alberta's boreal forest. *Forest Ecology*
640 *and Management, 409*, 29-37
641 Mateo, R.G., Mokany, K., & Guisan, A. (2017). Biodiversity Models: What If Unsaturation Is
642 the Rule? *Trends in Ecology & Evolution, 32*, 556-566
643 McCune, B. (1994). Improving community analysis with the Beals smoothing function.
644 *Écoscience, 1*, 82-86
645 McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat
646 load. *Journal of Vegetation Science, 13*, 603-606
647 Moeslund, J., Arge, L., & Bøcher, P. (2013). Topographically controlled soil moisture is the
648 primary driver of local vegetation patterns across a lowland region. Ecosphere 4. In
649 Moeslund, J.E., Brunbjerg, A.K., Clausen, K.K., Dalby, L., Fløjgaard, C., Juel, A., & Lenoir, J.
650 (2017). Using dark diversity and plant characteristics to guide conservation and restoration.
651 *Journal of Applied Ecology, 54*, 1730-1741
652 Moeslund, J.E., Zlinszky, A., Ejrnæs, R., Brunbjerg, A.K., Bøcher, P.K., Svenning, J.-C., &
653 Normand, S. (2019). Light detection and ranging explains diversity of plants, fungi, lichens, and

654 bryophytes across multiple habitats and large geographic extent. *Ecological Applications, 29*,
655 e01907
656 Mokany, A., & Shine, R. (2003). Competition between tadpoles and mosquito larvae. *Oecologia,*
657 *135*, 615-620
658 Mueller, G.M. (2011). *Biodiversity of fungi: inventory and monitoring methods*. Elsevier
659 Münzbergová, Z., & Herben, T. (2004). Identification of suitable unoccupied habitats in
660 metapopulation studies using co□occurrence of species. *Oikos, 105*, 408-414
661 Nadeau, M.B., & Sullivan, T.P. (2015). Relationships between plant biodiversity and soil fertility
662 in a mature tropical forest, Costa Rica. *International Journal of Forestry Research, 2015*, 1-13
663 Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., &
664 Kennedy, P.G. (2016). FUNGuild: an open annotation tool for parsing fungal community
665 datasets by ecological guild. *Fungal Ecology*, *20*, 241-248
666 Nordén, B., & Paltto, H. (2001). Wood-decay fungi in hazel wood: species richness correlated to
667 stand age and dead wood features. *Biological Conservation, 101*, 1-8
668 Nordén, B., Ryberg, M., Götmark, F., & Olausson, B. (2004). Relative importance of coarse and
669 fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests.
670 *Biological Conservation, 117*, 1-10
671 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R., Simpson, G.L.,
672 Solymos, P., Stevens, M., & Wagner, H. (2017). vegan: Community Ecology Package. R
673 package version 2.4-3
674 Pärtel, M. (2014). Community ecology of absent species: hidden and dark diversity. *Journal of*
675 *Vegetation Science, 25*, 1154-1159

676 Pärtel, M., Öpik, M., Moora, M., Tedersoo, L., Szava-Kovats, R., Rosendahl, S., Rillig, M.C.,
677 Lekberg, Y., Kreft, H., Helgason, T., Eriksson, O., Davison, J., Bello, F., Caruso, T., & Zobel,
678 M. (2017a). Historical biome distribution and recent human disturbance shape the diversity of
679 arbuscular mycorrhizal fungi. *New Phytologist, 216*, 227-238
680 Pärtel, M., Szava-Kovats, R., & Zobel, M. (2011). Dark diversity: shedding light on absent
681 species. *Trends in Ecology & Evolution, 26*, 124-128
682 Pärtel, M., Szava-Kovats, R., & Zobel, M. (2013). Community completeness: linking local and
683 dark diversity within the species pool concept. *Folia Geobotanica, 48*, 307-317
684 Pärtel, M., Zobel, M., Öpik, M., & Tedersoo, L. (2017b). Global patterns in local and dark
685 diversity, species pool size and community completeness in ectomycorrhizal fungi. In L.
686 Tedersoo (Ed.), *Biogeography of Mycorrhizal Symbiosis* (pp. 395-406). Cham, Switzerland:
687 Springer International Publishing
688 Pärtel, M., Zobel, M., Zobel, K., & van der Maarel, E. (1996). The species pool and its relation
689 to species richness: Evidence from estonian plant communities. *Oikos, 75*, 111-117
690 Pellkofer, S., van der Heijden, M.G.A., Schmid, B., & Wagg, C. (2016). Soil Communities
691 Promote Temporal Stability and Species Asynchrony in Experimental Grassland Communities.
692 *PLOS ONE, 11*, e0148015
693 Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M.R., Gossner, M.M., Seibold, S., Simons,
694 N.K., Schall, P., van der Plas, F., Manning, P., Manzanedo, R.D., Boch, S., Prati, D., Ammer, C.,
695 Bauhus, J., Buscot, F., Ehbrecht, M., Goldmann, K., Jung, K., Müller, J., Müller, J.C., Pena, R.,
696 Polle, A., Renner, S.C., Ruess, L., Schönig, I., Schrumpf, M., Solly, E.F., Tschapka, M.,
697 Weisser, W.W., Wubet, T., & Fischer, M. (2019). Specialisation and diversity of multiple trophic
698 groups are promoted by different forest features. *Ecology letters, 22*, 170-180

699 Peura, M., Gonzalez, R.S., Müller, J., Heurich, M., Vierling, L.A., Mönkkönen, M., & Bässler,
700 C. (2016). Mapping a 'cryptic kingdom': Performance of lidar derived environmental variables
701 in modelling the occurrence of forest fungi. *Remote Sensing of Environment, 186*, 428-438
702 Pfeifer, N., Mandlburger, G., Otepka, J., & Karel, W. (2014). OPALS–A framework for
703 Airborne Laser Scanning data analysis. *Computers, Environment and Urban Systems, 45*, 125-
704 136
705 R Core Team (2019). R: A language and environment for statistical computing In. Vienna,
706 Austria: https://www.R-project.org/
707 Ricotta, C. (2005). Through the Jungle of Biological Diversity. *Acta Biotheoretica, 53*, 29-38
708 Ricotta, C. (2007). A semantic taxonomy for diversity measures. *Acta Biotheoretica, 55*, 23-33
709 Riibak, K., Ronk, A., Kattge, J., & Pärtel, M. (2017). Dispersal limitation determines
710 large□scale dark diversity in Central and Northern Europe. *Journal of Biogeography, 44*, 1770-
711 1780
712 Ronk, A., Szava□Kovats, R., & Pärtel, M. (2015). Applying the dark diversity concept to plants
713 at the European scale. *Ecography, 38*, 1015-1025
714 Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., &
715 Fierer, N. (2010). Soil bacterial and fungal communities across a pH gradient in an arable soil.
716 *The ISME journal, 4*, 1340
717 Rousk, J., Brookes, P.C., & Bååth, E. (2009). Contrasting soil pH effects on fungal and bacterial
718 growth suggest functional redundancy in carbon mineralization. *Applied and Environmental*
719 *Microbiology, 75*, 1589-1596
720 Sarkar, S., & Margules, C. (2002). Operationalizing biodiversity for conservation planning.
721 *Journal of Biosciences, 27*, 299-308

722 Scott, C.E., Alofs, K.M., & Edwards, B.A. (2011). Putting dark diversity in the spotlight. *Trends*
723 *in Ecology & Evolution, 26*, 263-264
724 Silvertown, J., Araya, Y., & Gowing, D. (2015). Hydrological niches in terrestrial plant
725 communities: a review. *Journal of Ecology, 103*, 93-108
726 Solow, A.R., & Polasky, S. (1994). Measuring biological diversity. *Environmental and*
727 *Ecological Statistics, 1*, 95-103
728 Staddon, P.L., Thompson, K., Jakobsen, I., Grime, J.P., Askew, A.P., & Fitter, A.H. (2003).
729 Mycorrhizal fungal abundance is affected by long-term climatic manipulations in the field.
730 *Global Change Biology, 9*, 186-194
731 Sterkenburg, E., Bahr, A., Brandström Durling, M., Clemmensen, K.E., & Lindahl, B.D. (2015).
732 Changes in fungal communities along a boreal forest soil fertility gradient. *New Phytologist, 207*,
733 1145-1158
734 Su, J.G., & Bork, E.W. (2007). Characterization of diverse plant communities in Aspen Parkland
735 rangeland using LiDAR data. *Applied Vegetation Science, 10*, 407-416
736 Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V.,
737 Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A.,
738 Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C.,
739 Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H.,
740 Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H.,
741 Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L.-d., Greslebin, A., Grelet,
742 G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang,
743 T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., & Abarenkov, K.
744 (2014). Global diversity and geography of soil fungi. *Science, 346*, 1256688

745 Thers, H., Brunbjerg, A.K., Læssøe, T., Ejrnæs, R., Bøcher, P.K., & Svenning, J.-C. (2017).
746 Lidar-derived variables as a proxy for fungal species richness and composition in temperate
747 Northern Europe. *Remote Sensing of Environment, 200*, 102-113
748 Tonn, N., & Ibáñez, I. (2017). Plant-mycorrhizal fungi associations along an urbanization
749 gradient: implications for tree seedling survival. *Urban Ecosystems, 20*, 823-837
750 Townsend, C.R., Scarsbrook, M.R., & Dolédec, S. (1997). The intermediate disturbance
751 hypothesis, refugia, and biodiversity in streams. *Limnology and oceanography, 42*, 938-949
752 Turner, G.D., Lewis, J.D., Mates-Muchin, J.T., Schuster, W.F., & Watt, L. (2009). Light
753 availability and soil source influence ectomycorrhizal fungal communities on oak seedlings
754 grown in oak- and hemlock-associated soilsContribution No. 225 of the Louis Calder Center and
755 Biological Station, Fordham University, Armonk, New York. *Canadian Journal of Forest*
756 *Research, 39*, 1247-1258
757 Twieg, B.D., Durall, D.M., & Simard, S.W. (2007). Ectomycorrhizal fungal succession in mixed
758 temperate forests. *New Phytologist, 176*, 437-447
759 Unterseher, M., & Tal, O. (2006). Influence of small scale conditions on the diversity of wood
760 decay fungi in a temperate, mixed deciduous forest canopy. *Mycological Research, 110*, 169-178
761 Valdez, J.W., Hartig, F., Fennel, S., & Poschlod, P. (2019). The recruitment niche predicts plant
762 community assembly across a hydrological gradient along plowed and undisturbed transects in a
763 former agricultural wetland. *Frontiers in plant science, 10*, 88
764 Vehmas, M., Eerikäinen, K., Peuhkurinen, J., Packalén, P., & Maltamo, M. (2009). Identification
765 of boreal forest stands with high herbaceous plant diversity using airborne laser scanning. *Forest*
766 *Ecology and Management, 257*, 46-53

767 Wang, J., Chen, C., Ye, Z., Li, J., Feng, Y., & Lu, Q. (2018). Relationships Between Fungal and
768 Plant Communities Differ Between Desert and Grassland in a Typical Dryland Region of
769 Northwest China. *Frontiers in Microbiology, 9*
770 Xiong, S.J., Johansson, M.E., Hughes, F.M.R., Hayes, A., Richards, K.S., & Nilsson, C. (2003).
771 Interactive effects of soil moisture, vegetation canopy, plant litter and seed addition on plant
772 diversity in a wetland community. *Journal of Ecology, 91*, 976-986
773 Yahr, R., Schoch, C.L., & Dentinger, B.T. (2016). Scaling up discovery of hidden diversity in
774 fungi: impacts of barcoding approaches. *Philosophical Transactions of the Royal Society B:*
775 *Biological Sciences, 371*, 20150336
776 Yang, G., Wagg, C., Veresoglou, S.D., Hempel, S., & Rillig, M.C. (2018). How Soil Biota Drive
777 Ecosystem Stability. *Trends in Plant Science, 23*, 1057-1067
778 Yang, T., Adams, J.M., Shi, Y., He, J.-s., Jing, X., Chen, L., Tedersoo, L., & Chu, H. (2017).
779 Soil fungal diversity in natural grasslands of the Tibetan Plateau: associations with plant
780 diversity and productivity. *New Phytologist, 215*, 756-765
781 Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., & Tilman, D. (2003). Plant diversity, soil
782 microbial communities, and ecosystem function: Are there any links? *Ecology, 84*, 2042-2050
783 Zlinszky, A., Schroiff, A., Kania, A., Deák, B., Mücke, W., Vári, Á., Székely, B., & Pfeifer, N.
784 (2014). Categorizing grassland vegetation with full-waveform airborne laser scanning: A
785 feasibility study for detecting Natura 2000 habitat types. *Remote Sensing, 6*, 8056-8087
786 Zobel, M. (2016). The species pool concept as a framework for studying patterns of plant
787 diversity. *Journal of Vegetation Science, 27*, 8-18

788 Zuo, X., Wang, S., Lv, P., Zhou, X., Zhao, X., Zhang, T., & Zhang, J. (2016). Plant functional
789 diversity enhances associations of soil fungal diversity with vegetation and soil in the restoration
790 of semiarid sandy grassland. *Ecology and Evolution, 6*, 318-328

791