

The critical role of tree species and human disturbance in determining the macrofungal diversity in Europe

Haili Yu¹  | Tiejun Wang¹  | Andrew Skidmore^{1,2}  | Marco Heurich^{3,4}  | Claus Bässler^{4,5} 

¹Faculty of Geo-Information Science and Earth Observation, University of Twente, Enschede, The Netherlands

²Department of Earth and Environmental Science, Macquarie University, Sydney, New South Wales, Australia

³Chair of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany

⁴Bavarian Forest National Park, Grafenau, Germany

⁵Institute for Ecology, Evolution and Diversity, Faculty of Biological Sciences, Goethe University Frankfurt, Frankfurt, Germany

Correspondence

Haili Yu, Faculty of Geo-Information Science and Earth Observation, University of Twente, Hengelosestraat 99, 7514 AE Enschede, The Netherlands.
Email: h.yu-1@utwente.nl

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Abstract

Aim: Knowledge concerning species distribution is important for biodiversity conservation and environmental management. Fungi form a large and diverse group of species and play a key role in nutrient cycling and carbon storage. However, our understanding of fungal diversity and distribution remains limited, particularly at large spatial scales. Here, we predicted the diversity and distribution of ectomycorrhizal and saprotrophic macrofungi at relatively fine spatial resolution at a continental scale and examined the importance of variables that affect the distribution of these two functional groups.

Location: Europe.

Time period: 1990–2018.

Major taxa studied: Macrofungi.

Methods: From observations of 1,845 macrofungal species, we predicted the diversity and distribution of two functional groups of macrofungi at a resolution of 5 km across eight European countries based on 25 environmental variables using the MAXENT model. We determined the importance of variables that affect the distribution of these two functional groups of macrofungi using the built-in jackknife test in the model.

Results: Analysis of the modelling results showed that eastern Denmark and southern Sweden are biodiversity hotspots for both functional groups of macrofungal species. Tree species and human disturbance (i.e., the human footprint index) were found to be the two most important predictor variables explaining the distribution of ectomycorrhizal and saprotrophic macrofungi.

Main conclusions: Overall, our study demonstrates that tree species and human disturbance have played a more important role than climatic factors in determining the diversity and distribution of macrofungi at the continental scale. Our study suggests that fungal diversity and distribution might change considerably if the strongest predictors (i.e., tree species) were to be affected by climate change and/or human activity. Changes in fungal diversity might, in turn, influence other processes, because

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fungi are important in driving ecosystem processes, such as nutrient and carbon cycling.

KEYWORDS

abiotic factors, biotic factors, climatic variables, ectomycorrhizal, functional group, saprotrophic, species distribution model

1 | INTRODUCTION

The measurement and understanding of species diversity and distribution forms a central topic in ecology and biogeography (Gaston, 2000). Knowledge of the distribution of species and explaining the factors that drive this spatial distribution at different spatial scales are essential for biodiversity conservation, especially in the context of global change (Bellard et al., 2012; Purvis & Hector, 2000). However, compared with animals and plants, the fungal kingdom is little studied, especially at the continental level (Willis, 2018).

Fungi are one of the most diverse groups of organisms on Earth (Blackwell, 2011; Tedersoo et al., 2014). They are essential organisms that interact with the abiotic and biotic environment, regulating nutrient and carbon cycles. Macrofungi are those fungi that produce visible fruiting bodies. They form an important part of the fungal kingdom, which is estimated to comprise 53,000–110,000 species world-wide (Mueller et al., 2007). Ecologically, macrofungi can be classified as parasites, saprotrophs or symbiotic (mycorrhizal) species. The two main functional groups of macrofungi associated with global nutrient and carbon cycles are ectomycorrhizal fungi (mutualistic fungi) and saprotrophic fungi (Dighton, 2016). Ectomycorrhizal fungi live mutualistically with tree species and provide some benefit to their host. As symbionts, ectomycorrhizal fungi are involved in various mutualistic associations, contributing to the uptake of water, nitrogen, phosphorus or other minerals from the soil to their host; hence, they underpin primary production in natural ecosystems (Dighton, 2016; Read, 1991). Saprotrophic fungi are fungi that use non-living organic matter, such as dead plants and animals; they are decomposers in the ecosystem. These saprotrophic fungi can release nutrients and energy stored in dead organisms, supporting the crucial process of nutrient cycling and partaking in the global carbon cycle (Dighton, 2016). They form the basis of soil food chains and play an indispensable role in the quest for sustainable development (Palm & Chapela, 1997). Many macrofungal species also form a food source for humans and wild animals, contributing to human welfare directly and indirectly (Boa, 2004). Despite their essential roles, the distribution pattern of macrofungi has rarely been explored in macroecology, and our knowledge of factors determining their distribution remains limited.

For ectomycorrhizal fungi, multiple local-scale studies have shown that soil nutrients and host tree species form the key factors influencing their diversity and distribution (Bahram et al., 2012; Ishida et al., 2007; Toljander et al., 2006). At the continental scale, Andrew, Halvorsen, et al. (2018) showed that climate (e.g., mean

annual temperature) was strongly correlated with the ectomycorrhizal macrofungal assemblage in Europe. In contrast, using a root-tip sampling method based on Sanger sequencing technology, van der Linde et al. (2018) found that host-related variables contributed more to explaining the continental-scale diversity pattern of ectomycorrhizal fungi than did climatic variables in Europe. The role of tree species and the relative importance of tree species versus climatic variables in determining the diversity and distribution of ectomycorrhizal fungi at a large spatial scale remain largely unexplored.

Regarding saprotrophic fungi, some local-scale studies showed that microclimate (temperature and humidity), resource availability (such as the amount of available dead wood) and host tree species were the most important factors determining their diversity (Bässler et al., 2010; Rayner & Boddy, 1988; Wollan et al., 2008). Some large-scale studies across Europe have shown that climate was the most crucial variable influencing their diversity (Andrew, Halvorsen, et al., 2018) and that there was no significant relationship between tree species and the diversity of saprotrophic macrofungi (Andrew, Büntgen, et al., 2019; Andrew, Halvorsen, et al., 2018). However, other studies provided evidence that saprotrophic fungal diversity was correlated with tree species (Baber et al., 2016; Purahong et al., 2018). Further studies need to be carried out to improve our understanding of the role of tree species in determining the diversity and distribution of saprotrophic macrofungi at a large spatial scale.

Macrofungi are far more challenging to collect than plants and animals, because the presence of fruiting bodies is usually seasonal and ephemeral, and the sampling of cryptic macrofungi can be time consuming and laborious (Mueller et al., 2004). For a long time, attempts to study fungi at a large spatial scale were hindered by the lack of data compilation and integration (Willis, 2018). Thanks to the development of DNA sequencing technology, scientists can rely on the indirect method, involving the isolation of spores and/or mycelia in the environment from soil samples, to study the fungal diversity at continental and even global scales (van der Linde et al., 2018; Tedersoo et al., 2014). However, some researchers suggest that such studies might need to be verified using various data sources and more comprehensive spatial gradients (Andrew, Büntgen, et al., 2019). For example, Porter et al. (2008) showed that the assemblage of fungi at the species level detected from fruiting bodies and soil samples is substantially different. An ideal complement to molecular data might be fungal data from open-source biodiversity data. These freely accessible databases offer access to biodiversity information in the form of species occurrences (Hochmair et al., 2020), in which observations of fungal species are becoming increasingly available worldwide (Andrew, Diez, et al., 2019). Macrofungal occurrence data have

been collected by amateur mycologists, naturalists and researchers for several hundred years, especially in Europe, which has more data available than any other region (Andrew, Diez, et al., 2019; Mueller et al., 2007). These data form a prime source of knowledge regarding fungal diversity and distribution (Andrew, Diez, et al., 2019).

Knowledge of species diversity and distribution has greatly improved as a result of the increasing availability of open biodiversity data (Maldonado et al., 2015) and the emergence of new techniques to analyse such information (Guisan & Zimmermann, 2000; Wollan et al., 2008). Species distribution models (SDMs; also known as ecological niche models, bioclimatic envelope models and habitat suitability models) are numerical tools that combine species occurrence data with environmental estimates. They are popular tools in quantitative ecology and are used to gain ecological and evolutionary insights and predict the distribution of species across landscapes (Elith & Leathwick, 2009). Given the increasing availability of extensive spatial environmental data and the growing sophistication of modelling algorithms, SDMs are widely used for various biological groups in the terrestrial, marine and freshwater realms (Cacciapaglia & van Woesik, 2015; Mateo et al., 2016; Niittynen et al., 2020; Oberdorff et al., 2019; Thuiller et al., 2014; Williams et al., 2009). Although this technique is commonly applied to terrestrial vascular plants and animals, its application to the fungal kingdom remains relatively rare (Elith & Leathwick, 2009; Větrovský et al., 2019; Wollan et al., 2008).

In this study, by taking advantage of openly available biodiversity data, we aimed to determine the relative importance of biotic, abiotic and anthropogenic factors at a fine spatial resolution in predicting the diversity and distribution of macrofungi on a continental scale. Specifically, our aims were as follows: (1) to predict the distribution of two different functional groups of macrofungi (i.e., ectomycorrhizal and saprotrophic macrofungi) at a 5 km spatial resolution from southern Spain to northern Norway, based on a comprehensive set of environmental variables using presence-only SDMs; and (2) to examine the importance of variables that affect the distribution of two different functional groups of macrofungi at the European scale.

2 | MATERIALS AND METHODS

2.1 | Occurrence data of macrofungal species

For most regions, systematic biological survey data with both presence and absence information for species are often scarce and/or limited in coverage. The Global Biodiversity Information Facility (GBIF; <http://data.gbif.org>) is an international network devoted to making the world's biodiversity data publicly available. It is currently the largest database of species occurrence observations, gathering species records from different sources (e.g., museums, herbaria, survey projects, collections of individual researchers, citizen science) and other biodiversity platforms world-wide (Chandler et al., 2017; Hochmair et al., 2020). These databases embody the long-term public and private investment in biological science and are hugely important sources of species occurrence data (Elith et al., 2011). The GBIF

defines standards for publishing data and metadata, and all occurrence records indexed on the GBIF must satisfy certain data-quality criteria before being included in the platform (GBIF.org, 2020). According to data-quality requirements, data are published initially as primary occurrence records on GBIF in a standardized format. Then, GBIF performs additional checks to verify data formats, data quality and their suitability for use. To date, the GBIF network has collected > 21 million occurrence records of fungi across the globe.

For our analysis, we downloaded georeferenced fungal occurrence records from eight European countries (i.e., Finland, France, Spain, Germany, Norway, The Netherlands, Denmark and Sweden) from GBIF that contained a relatively large amount of fungal occurrence data, which were provided mainly by comparatively authoritarian organizations (e.g., museum, university project or biodiversity centre; see Supporting Information Appendix S1). To include as many species as possible in our study and match the corresponding environmental data layer, we extracted the records collected between 1990 and 2018, a period during which there was a relatively stable number of fungal species (Supporting Information Appendix S2: Figure S2.1).

The majority of the macromycetes are in taxa from the phylum Basidiomycota, subphylum Agaricomycotina (Porter et al., 2008). The Agaricomycetes is a conspicuous group of fungi under the subphylum Agaricomycotina, presenting striking diversity in fruiting bodies and comprising ecologically diverse species with equally diverse functional roles (Sánchez-García et al., 2020). There were seven orders under the Agaricomycetes class with a number of species ranking in the top 10 orders in our database, namely the Agaricales, Boletales, Cantharellales, Hymenochaetales, Polyporales, Russulales and Thelephorales. These orders represent > 80% of species in the phylum Basidiomycota in our original database (Supporting Information Appendix S2: Figure S2.2). We therefore screened the species in these seven orders to select macrofungal species to use in our study. The following procedures were implemented on this subset.

Across the eight European countries, 5 km × 5 km grids were generated, based on the European Terrestrial Reference System 1989 (ETRS89) datum and Lambert azimuthal equal area (LAEA) projection (EPSG: 3035) used by the European Environment Agency (EEA, <https://www.eea.europa.eu/>). To improve the consistency and usability of the GBIF data in our study, we filtered and culled the fungal dataset using ArcGIS v.10.7.1 (ESRI, Redlands, CA, USA) and the "raster" package (Hijmans, 2020) in R v.3.6.1 (R Core Team, 2013). We removed records without a specific species name and/or flagged with taxonomic issues by GBIF; we disregarded fungal records with "coordinate uncertainty in meter" > 5 km. We rarefied records spatially by eliminating all but one point present per species within each 5 km × 5 km grid cell, to avoid double counting of the presence of each species and to reduce overfitting to sampling bias in SDMs (Boria et al., 2014; Kramer-Schadt et al., 2013). Furthermore, we removed species recorded in < 30 grid cells (of 5 km × 5 km) (Wisz et al., 2008) to safeguard the validity of the predictive performance of the SDMs and ensure access to a reasonable number of test data for modelling.

Given that our study focused on two nutritional modes (i.e., saprotrophic and ectomycorrhizal), we compiled checklists of nutritional mode at the species level based on the database published by Andrew, Heegaard, et al. (2018), Sánchez-García et al. (2020) and Nguyen et al. (2016), in addition to genus-level databases published by Rinaldi et al. (2008) and Tedersoo and Smith (2013). Initially, we assigned a nutritional mode value to records according to the species-level checklist; then, for the rest of the species without species-level nutritional mode information, we assigned their nutritional mode according to the genus-level checklist. To ensure the nutritional mode of species with genus-level information, we checked their nutritional mode carefully. Most species within the same genera have a similar lifestyle. However, there are still exceptions, such as species with unsolved lifestyles in the genera of *Entoloma*, *Volvariella*, *Clitopilus* and *Arrhenia*. We removed species in these genera to ensure our assignment of the fungal nutritional mode at genus level.

As a result, a total of 1,845 species (i.e., 774 ectomycorrhizal macrofungal species and 1,071 saprotrophic macrofungal species) with 878,978 occurrence records were extracted for our modelling, of which > 50% of the species were found in at least seven countries in our study area (Supporting Information Appendix S2: Figure S2.2c). The detailed occurrence statistics are presented per country in Table 1 and the Supporting Information (Appendix S2: Tables S2.1 and S2.2). The distribution of the occurrence data is depicted in Figure 1.

2.2 | Predictor variables

2.2.1 | Climate

We obtained 19 bioclimatic variables (v.2.0) from the WorldClim database (<http://www.worldclim.org/>) at a resolution of c. 5 km (Supporting Information Appendix S3: Table S3.1). These bioclimatic variables were derived from the monthly precipitation and temperature values between 1970 and 2000 and processed further to generate more biologically meaningful variables, such as annual trends, seasonality and extreme factors determining the species niches (Fick & Hijmans, 2017).

2.2.2 | Soil

We chose eight soil properties from the topsoil layer (0–30 cm) that characterize the fertility, soil water and rooting conditions to represent important chemical and physical soil factors regarding growth of fungi. The soil organic carbon data were downloaded from the European Soil Data Centre (ESDAC; Panagos et al., 2012) (<https://esdac.jrc.ec.europa.eu/themes/soil-organic-carbon-content>), and the other seven soil factors were extracted from the gridded global soil dataset for use in earth system models (Shangguan et al., 2014) (<https://cmr.earthdata.nasa.gov/search/concepts/C121460404>

TABLE 1 The number of saprotrophic and ectomycorrhizal macrofungal species in eight European countries

Country	Number of ectomycorrhizal species used in modelling	Number of saprotrophic species used in modelling	Source
Finland	416	616	GBIF.org (7 December 2018) GBIF Occurrence Download https://doi.org/10.15468/dl.cbs3ys
France	627	917	GBIF.org (16 January 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.log0qg
Spain	564	872	GBIF.org (17 January 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.9pjyeg
Germany	637	990	GBIF.org (17 January 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.wbuq93
Norway	647	898	GBIF.org (23 November 2018) GBIF Occurrence Download https://doi.org/10.15468/dl.vjjigy
Netherlands	395	735	GBIF.org (16 January 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.fnarp9
Denmark	581	952	GBIF.org (28 November 2018) GBIF Occurrence Download https://doi.org/10.15468/dl.w773at
Sweden	731	1,002	GBIF.org (7 December 2018) GBIF Occurrence Download https://doi.org/10.15468/dl.wisfph
Total	774	1,071	

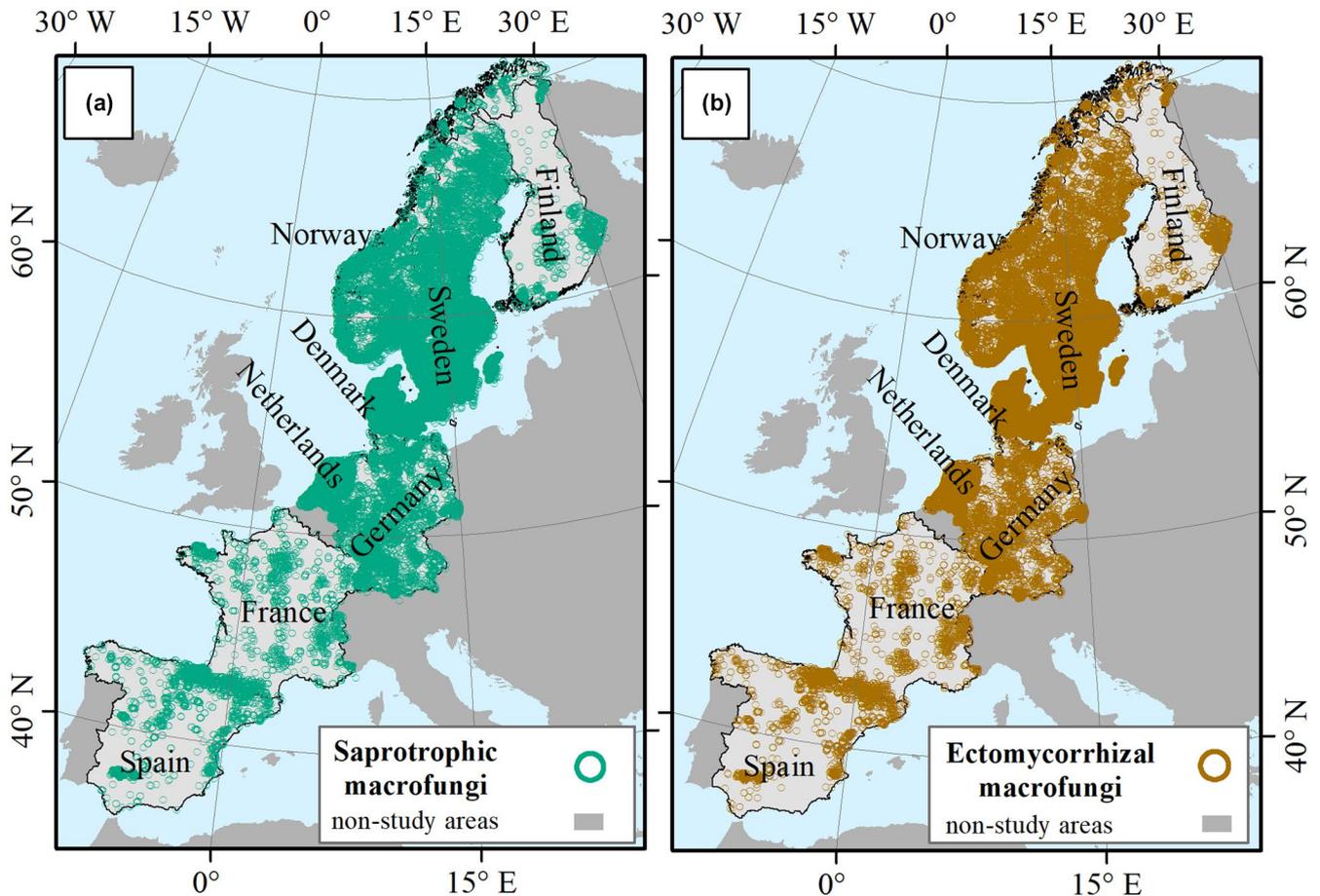


FIGURE 1 Location of the study area in Europe and the distribution of (a) saprotrophic macrofungi and (b) ectomycorrhizal macrofungi occurrence data used in this study

4-SCIOPS.html); all these original data were available at a resolution of c. 1 km.

2.2.3 | Vegetation

We took into account a wide range of vegetation-related variables, such as dominant tree species, tree cover density, forest age, forest canopy height and satellite-derived vegetation indices (Supporting Information Appendix S3: Table S3.1).

First, we obtained 1 km × 1 km maps of the 20 dominant tree species over Europe from the European Forest Institute (EFI; <https://www.efi.int/knowledge/maps/treespecies>). Based on those tree species distribution maps (Brus et al., 2012), we calculated the richness and diversity of the selected tree species in each 5 km grid cell using the “vegan” package (Dixon, 2003) in R v.3.6.1 (R Core Team, 2013).

Next, we downloaded a satellite-derived tree cover density status product for 2012 from the Copernicus Land Monitoring Service website (<https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density>). This displayed the level of tree cover density in a range from 0 (no trees) to 100% (full canopy coverage) at a pan-European scale, with a spatial resolution of 100 m.

We also obtained a pan-European map depicting mean tree age at a resolution of c. 13 km for the time period 2000–2010 (<https://doi.org/10.6084/m9.figshare.c.3463902.v2>). This data layer formed a pan-European spatially explicit forest structure product (Moreno et al., 2017).

We downloaded forest canopy height data from the Spatial Data Access Tool (<https://webmap.ornl.gov/ogc>). This dataset represented global tree height based on a fusion of spaceborne-lidar data (2005) from the Geoscience Laser Altimeter System (GLAS) and ancillary geospatial data (Simard et al., 2011). For each 5 km grid cell, we calculated the mean and the standard deviation of the forest canopy height using Zonal Statistics in Spatial Analyst toolboxes in ArcGIS.

SPOT VEGETATION (VGT), a normalized difference vegetation index (NDVI) product derived from the Satellite Pour l'Observation de la Terre (SPOT) with a 1 km spatial resolution, was also used. We downloaded SPOT-VGT 10-day composite NDVI time series over a 12-year period (1999–2010) from the Copernicus Global Land Service website (<https://land.copernicus.eu/global/products/ndvi>). Initially, we first calculated one 12-month (January–December) time series NDVI by averaging the 12-year SPOT-VGT NDVI series. We then used an adaptive Savitzky–Golay smoothing filter to remove the noise in the averaged NDVI time series using the TIMESAT package

(Jönsson & Eklundh, 2004). Finally, we calculated the annual mean, minimum, maximum and standard deviation value of NDVI.

2.2.4 | Topography

We used the digital elevation model (DEM) data at c. 1 km resolution from the United States Geological Survey (USGS) Earth Resources Observation and Science (EROS) Data Center (<https://www.usgs.gov/centers/eros>) to compute topographic variables, such as elevation, slope and terrain curvature, using the Spatial Analyst toolbox for ArcGIS. For each 5 km grid cell, we calculated the standard deviations of elevation and slope, in addition to the curvature and range of slope using the Zonal Statistics tools from the Spatial Analyst toolbox in ArcGIS.

2.2.5 | Anthropogenic variables

In this study, we considered three anthropogenic variables: land-cover and land-use data, forest management approach and human footprint index.

We downloaded the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type (MCD12Q1) v.6 data from the NASA Land Processes Distributed Active Archive Center (<https://lpdaac.usgs.gov/products/mcd12q1v006/>). To ensure consistency of the data with other remote sensing-derived land-cover products, we followed the classification scheme used in the study by Tuanmu and Jetz (2014) and reclassified the MODIS land-cover data into their 12 categories.

We also obtained the European dominant forest management approach (FMA) data presented by Hengeveld et al. (2012). This dataset provided information about different stages in forest succession and could be used to imply forest disturbance and determine the services that the forest provided (Hengeveld et al., 2012).

Finally, we used the human footprint index (HFP; <https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic>) to represent the general influence of anthropogenic activities [Wildlife Conservation Society (WCS) & Center for International Earth Science Information Network (CIESIN) Columbia University, 2005]. The HFP index, ranging from zero (least influenced/most wild) to 100 (least wild), is seen as a surrogate for anthropogenic impacts on the environment and is created from a number of global data layers covering human population density, human land use and infrastructure, and human access (Sanderson et al., 2002).

In total, we selected 47 potential predictor variables covering five categories (i.e., climate, soil, vegetation, topography and anthropogenic influence; Table 2; Supporting Information Appendix S3: Table S3.1). We resampled variables with differing spatial resolutions to fit the 5 km grid using the Zonal Statistics tools from the Spatial Analyst toolbox in ArcGIS. For continuous variables (such as bioclimatic variables, NDVI, forest height and tree cover density), we used zonal statistics to calculate the mean raster value for each

5 km grid cell. For categorical variables (such as forest management approaches and land cover), we used zonal statistics to calculate the majority of the values in each 5 km grid cell.

2.2.6 | Collinearity analysis

Multicollinearity is a common feature of ecological data. It inflates the variance of regression parameters, potentially leading to bias and uncertainty in identifying relevant predictors in a statistical model (Dormann et al., 2013). To avoid potential multicollinearity issues in model fitting and reduce the redundancy of input predictor variables, we performed a correlation analysis. We calculated the Pearson correlation coefficient and created a correlation matrix using the “corrplot” package (Wei & Simko, 2017) in R v.3.6.1 (R Core Team, 2013) (Supporting Information Appendix S3: Figure S3.1). We retained variables with low correlation ($|r| < .7$) (Dormann et al., 2013). For those variables that were highly correlated ($|r| > .7$), we selected the variables that were most ecologically relevant to fungi based on expert knowledge and scientific literature (Dormann et al., 2013; Moore et al., 2011; Wollan et al., 2008). Ultimately, 25 of the 47 variables were selected for use in our model (Table 2).

2.3 | Species distribution modelling

Multiple SDMs have been proposed in the past two decades, with different methods depending on the type of species data (presence-absence or presence only). Maximum Entropy (MAXENT) is a program based on a machine-learning algorithm for modelling species distributions from presence-only species records (Phillips et al., 2006). It can handle complex interactions between predictor and response variables efficiently to produce a continuous estimate of habitat suitability values ranging from zero (least suitable) to one (most suitable) (Elith et al., 2006). MAXENT is considered to be able to cope well with sparse, irregularly sampled data to produce robust results (Kramer-Schadt et al., 2013). In comparison to many other algorithms used in species distribution modelling, MAXENT is much less sensitive to sample size and has the best predictive power across all sample sizes (Wisz et al., 2008). We ran all models with MAXENT v.3.4.4 software (Steven et al., 2017) in our study.

Given that absence data are not available in the macrofungal database, MAXENT requires additional data representing the range of environmental conditions in the modelled region. These data are known as background or pseudo-absence data and are usually generated randomly across the study area (Merow et al., 2013; Phillips et al., 2009). However, occurrence data in natural history museums and herbaria are often thought to be spatially biased in surveys (e.g., toward easily accessible areas), and these differences between occurrence collection distribution and random distribution of background sampling might lead to inaccurate models (Phillips & Dudik, 2008; Phillips et al., 2009). The bias introduced by the difference between occurrence collection and background sampling can be avoided by ensuring that the background sample reflects the same bias as the presence

TABLE 2 Summary of environmental variables used in modelling the distribution of macrofungi in this study

Category	Variable (units)	Variable abbreviation	Source	Resolution
Climate	Annual mean temperature (°C)	BIO01	WorldClim	c. 5 km
	Mean diurnal range (°C)	BIO02		
	Temperature seasonality (%)	BIO04		
	Mean temperature of wettest quarter (°C)	BIO08		
	Annual precipitation (mm)	BIO12		
	Precipitation seasonality (%)	BIO15		
	Precipitation of warmest quarter (mm)	BIO18		
Soil	Available water capacity class	AWC	Global Soil Dataset for use in Earth System Models	c. 1 km
	Cation exchange capacity (cmol/kg)	CEC		
	pH	PHK		
	Sand content (%)	SAND		
	Topsoil texture	TEXT		
	Organic carbon (%)	OC		
Vegetation	Tree age (age classes, in years)	Age	Moreno et al. (2017)	c. 13 km
	Dominant tree species	Dominantree	European Forest Institute	1 km
	Tree species diversity	SHANNON		
	Forest canopy height (m)	Foreh_avg	NASA Earthdata	1 km
	Standard deviation of canopy height (m)	Foreh_std		
	Annual average NDVI	NDVI_mean	Copernicus Land Monitoring Service	1 km
	Tree cover density (%)	Treedense	Copernicus Land Monitoring Service	100 m
Topography	Elevation (m)	Elevation_avg	USGS Earth Resources Observation and Science Center	c. 1 km
	Elevation range (m)	Elevation_rg		
Anthropogenic	Land cover	CLC	NASA's Land Processes DAAC	c. 5 km
	Forest management approaches	FML	Hengeveld et al. (2012)	1 km
	Human Footprint Index	HFP	NASA Earthdata	c. 1 km

data. Some studies show that biased background sampling can lead to much better predictive performance than random background sampling (Kramer-Schadt et al., 2013; Namyatova, 2020; Phillips & Dudík, 2008; Phillips et al., 2009). This option of sampling biased background data is implemented in MAXENT software by adding a bias grid, with which the cell values reflect sampling effort and give a weight to choose background data (Fourcade et al., 2014). However, explicitly biased sampling of background sites may not be possible owing to a lack of accurate information about spatial bias of the presence data; hence, instead of using our knowledge of the artificially created biases, we produced the bias grids using a widely used method (i.e., creating a two-dimensional Gaussian kernel density map; Fourcade et al., 2014; Guillaumot et al., 2019; Phillips et al., 2009) based on the coordinates of the occurrence points, with the "kde2d" function of the "MASS" package (Ripley et al., 2013) in R, on the extent of the modelled area. For each species, we chose 10,000 biased background points in the study area according to the kernel density estimation layer to generate "pseudo-absence" data. We set 10-fold cross-validation in the "replicates" option for testing the model performance of each species and checked the built-in jackknife test to measure the variable importance (Phillips et al., 2006).

To evaluate model performance, we used both threshold-independent and threshold-dependent methods in our study. With the threshold-independent method, we used the area under the receiver-operating characteristic curve (AUC), where higher values represented higher accuracy (Swets, 1988). Although AUC has been criticized, it is the standard method to assess prediction accuracy and has been used extensively in the species distribution modelling literature because of its threshold independence and the ease of interpreting its results (Elith et al., 2006; Massada et al., 2013; Phillips et al., 2006). As a threshold-dependent method, we used true skill statistics (TSS; Allouche et al., 2006) to evaluate the performance of the models.

2.4 | Calculating distribution probability and diversity of macrofungi

Using the MAXENT model, we predicted the distribution probability of each species across the study area. We calculated the average distribution probability of species having the same nutritional mode in each grid cell to produce the general distribution probability map for both saprotrophic macrofungi and ectomycorrhizal macrofungi.

To produce the species diversity map for both saprotrophic macrofungi and ectomycorrhizal macrofungi, we used the maximum of the sum of specificity (quantifying commission errors) and sensitivity (quantifying omission errors) (Max SSS) as a threshold to transform non-binary model output (continuous distribution probability values) into binary (presence/absence) predictions for each species. Max SSS can minimize the error rate of both commission and omission errors, which has been widely used in SDMs as a robust method for threshold selection when only presence data are available (Liu et al., 2013). The binary outcome of each species was summed per nutritional mode for each grid cell to yield the species richness of ectomycorrhizal and saprotrophic macrofungi separately. To show the latitudinal and longitudinal variation of species richness, we calculated the mean species richness of all grids at the same coordinate at an interval of 5 km along latitude and longitude, respectively, using the stacked binary map of the two functional groups.

3 | RESULTS

3.1 | Model performance

Overall, the models for both saprotrophic macrofungi and ectomycorrhizal macrofungi performed well, with a mean AUC of .88 and a

mean TSS of .69 for saprotrophic macrofungal species, and a mean AUC of .90 and a mean TSS of .72 for ectomycorrhizal macrofungal species (Figure 2). The standard deviation of the cross-validation is depicted in the Supporting Information (Appendix S3: Figure S3.2) to show the predictive uncertainty of the model.

3.2 | Predicted distribution and diversity of macrofungi in Europe

Of the whole study area, eastern Denmark and southern Sweden exhibited the highest average distribution probability for ectomycorrhizal and saprotrophic macrofungi (Figure 3). The predicted species richness for both functional groups also exhibited a similar pattern to the probability distribution, with a large area in France and Spain revealing relatively low species richness in comparison to Denmark and Sweden (Figure 4). The latitudinal variation of species richness showed considerably high richness for both ectomycorrhizal macrofungi and saprotrophic macrofungal species in the north-central part of our study area, with a slightly more northerly position of the highest ectomycorrhizal macrofungi richness compared with saprotrophic macrofungi. Unlike the latitudinal distribution, the richness of macrofungal species showed a relatively large variation in the longitude distribution, in particular for saprotrophic macrofungi.

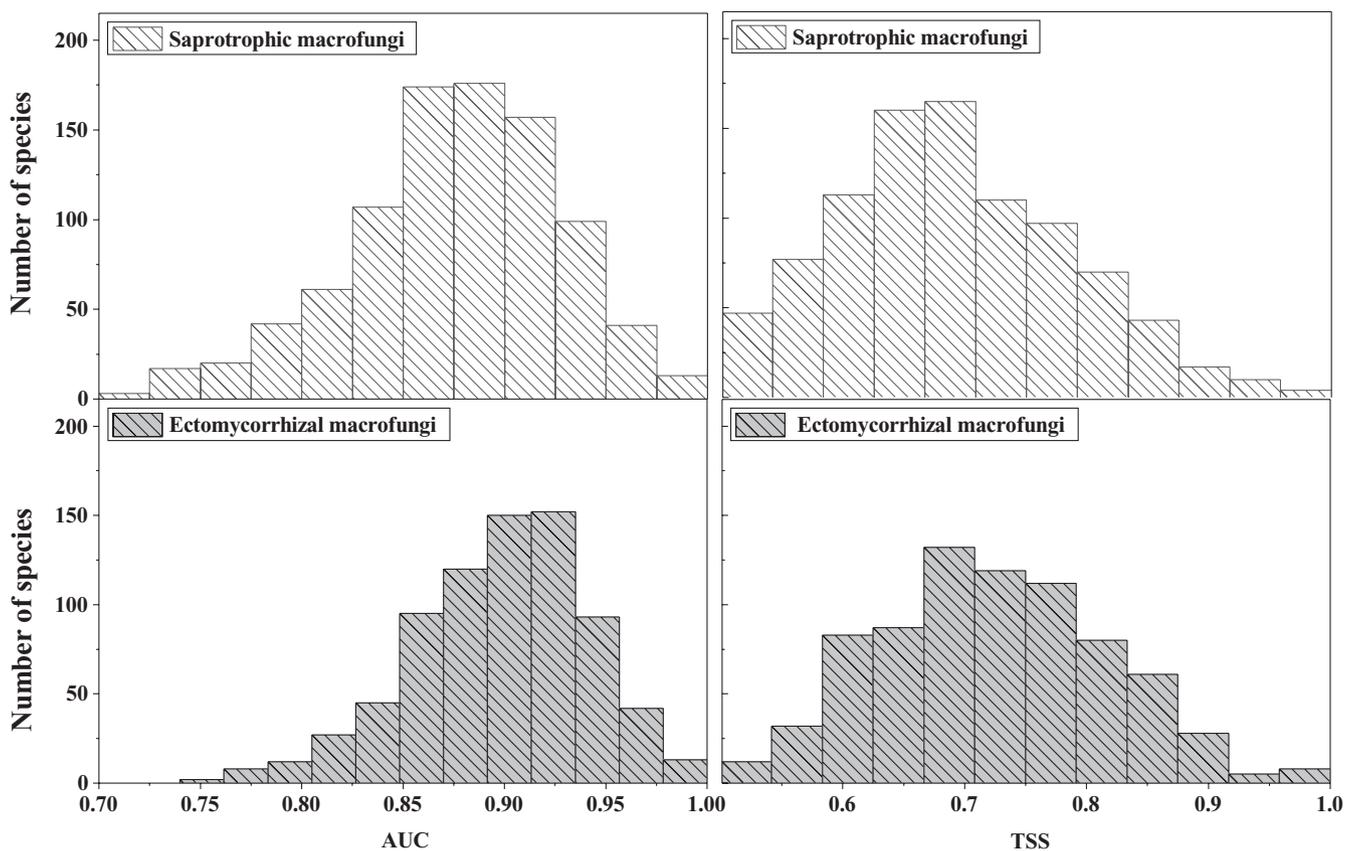


FIGURE 2 The frequency distribution of the area under the receiver-operating characteristic curve (AUC) and the true skill statistic (TSS) for two different functional groups of macrofungal species. Both AUC and TSS were used to evaluate the model performance for each individual species

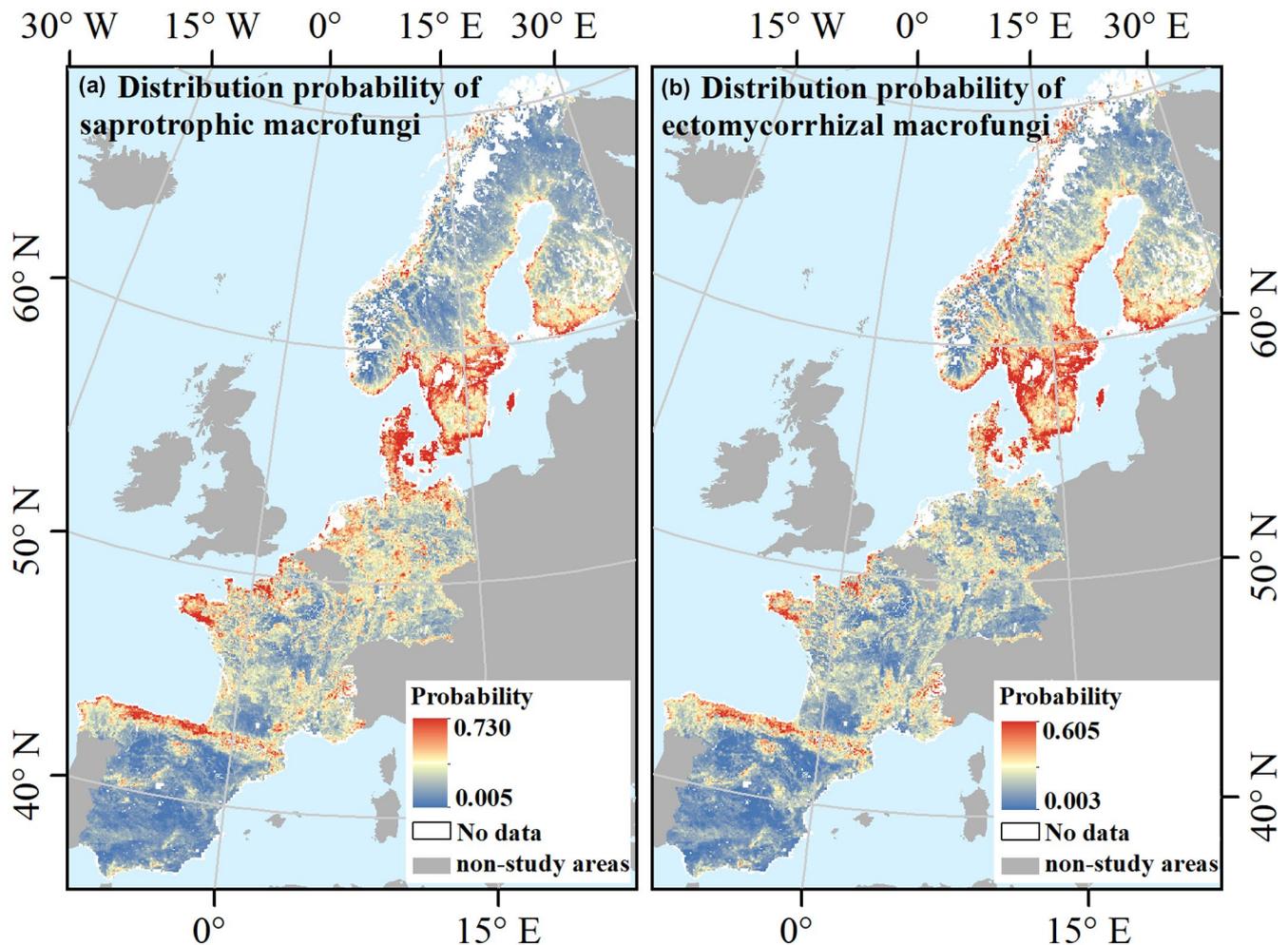


FIGURE 3 The average distribution probability per grid cell of (a) saprotrophic macrofungi species and (b) ectomycorrhizal macrofungi species

However, the main hotspots for the richness of ectomycorrhizal and saprotrophic macrofungi species remained predominantly concentrated in Denmark and southern Sweden.

3.3 | Factors affecting the diversity and distribution of macrofungi in Europe

The top three variables that contributed most among the 25 environmental factors used in our model were dominant tree species, human footprint index and tree cover density (Figure 5; Supporting Information Appendix S3: Figures S3.3 and S3.4). The distribution probability of both macrofungi groups varied for the 20 different dominant tree species, with a significantly ($p = .05$) higher distribution probability in areas dominated by *Fagus* spp. and *Picea* spp. Saprotrophic macrofungi showed the highest distribution probability in areas dominated by *Fagus* spp. (Figure 6a), whereas ectomycorrhizal macrofungi showed the highest distribution probability in areas dominated by *Picea* spp. (Figure 6d). We found an increasing richness with increasing tree cover density, which stabilized when the tree cover density exceeded a value of c. 30% (Figure 6c,f). The human footprint index also provided an important contribution to

the distribution of two functional groups of macrofungi (Figure 5). The response curve of the human footprint index showed that the distribution probability of both groups of macrofungi increased as the human footprint index rose (Figure 6b,e).

4 | DISCUSSION

This is the first fine-resolution (i.e., 5 km) study of macrofungi diversity and distribution at the continental scale, covering a broad latitudinal range from northern to southern Europe, taking a comprehensive set of environmental variables into consideration. We found that tree species and human disturbance appeared to be more important than climatic variables in influencing the diversity and distribution of macrofungi in Europe.

4.1 | Relative importance of tree species

Our results showed that vegetation-related variables, such as dominant tree species, tree cover density and forest age, provided a larger contribution to ectomycorrhizal macrofungi than climate.

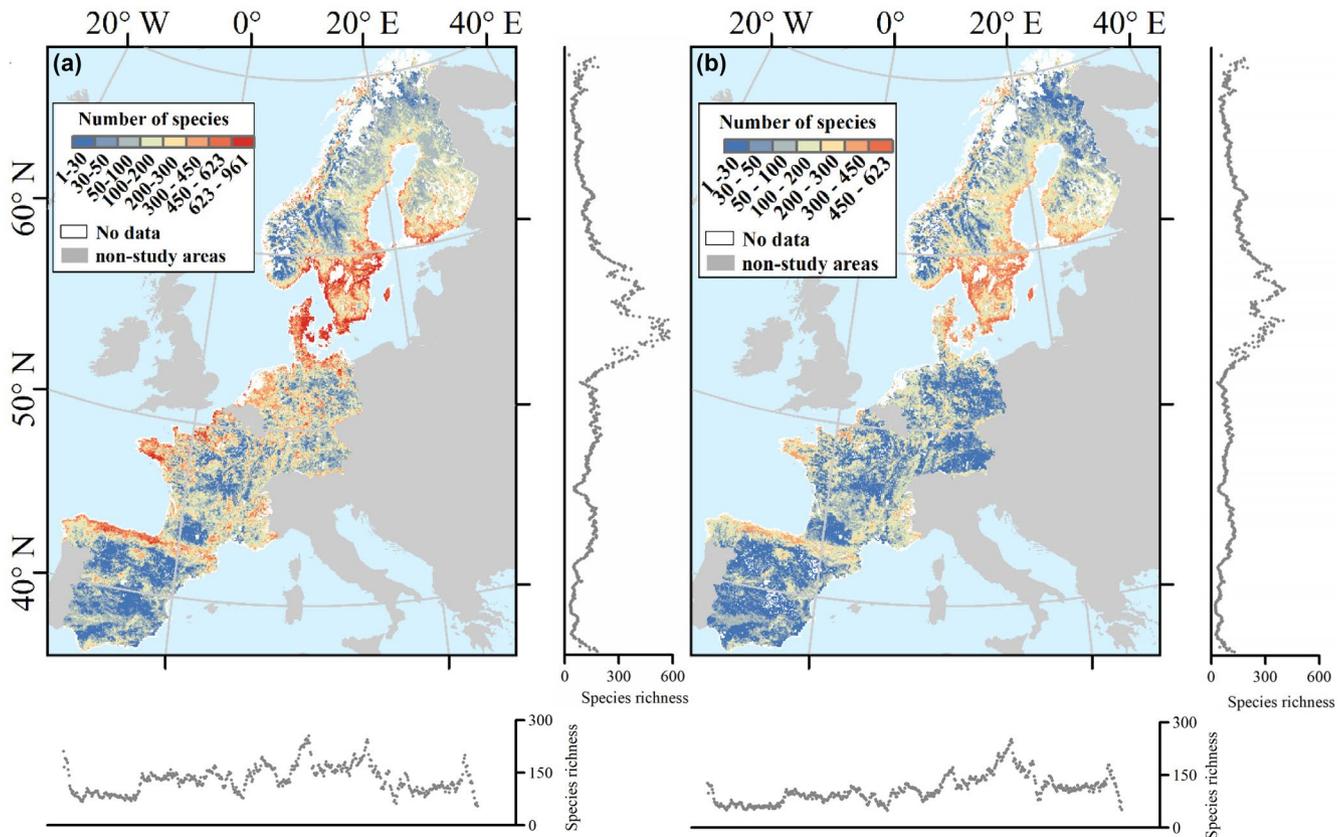


FIGURE 4 The distribution of the predicted number of species of two different functional groups of macrofungi, with the mean species richness at intervals of 5 km along latitude and longitude shown on the right and underneath. The number of species in each 5 km × 5 km grid for (a) saprotrophic macrofungi and (b) ectomycorrhizal macrofungi was calculated based on the macrofungal “presence” data, which were obtained by converting the continuous probability values into binary predictions (presence/absence) using a threshold of the maximum of the sum of specificity and sensitivity (Max SSS)

Ectomycorrhizal macrofungi were shown to have a significantly higher distribution probability in areas dominated by *Picea* spp. and *Fagus* spp. than in areas dominated by other tree species. Local and regional studies have also found tree species to be a key factor affecting the diversity and distribution of ectomycorrhizal fungal (Bahram et al., 2012; Ishida et al., 2007; Toljander et al., 2006). Spruce and beech are among the most important tree species of boreal and temperate forest, respectively, and support a very diverse community of fungal symbionts (Taylor et al., 2000). Many tree species might grow poorly or even fail to grow without the presence of ectomycorrhizas (Moore et al., 2011). However, at a continental and global level, climate rather than tree species was found to be the major factor driving the ectomycorrhizal macrofungal diversity (Andrew, Büntgen, et al., 2019; Tedersoo et al., 2014). Andrew, Büntgen, et al. (2019) found, using open-source macrofungal data, that climate, rather than tree species, was the prevailing driver shaping ectomycorrhizal fungal diversity patterns in central to northern Europe. However, their study was based on a grid size of 20 km × 20 km, which is much coarser than the grid used in our study. With such coarse spatial resolution, the detailed variation in biotic factors such as tree species composition might be blurred owing to the presence of a high proportion of small forest patches,

probably enhancing the role of climate. For example, in Central-West Europe > 45% of the forests are < 10,000 ha (a grid size of 10 km × 10 km) (Köhl & Linser, 2020). The environmental variables driving species diversity can be different depending on the spatial scale, including both the extent and the resolution (grain size) over which species diversity is measured (Guisan & Thuiller, 2005; Willis & Whittaker, 2002).

At the continental level, van der Linde et al. (2018) examined ectomycorrhizas by DNA sequencing from root tips from 137 plots and found that host tree species, rather than climate, explained ectomycorrhizal fungal community variance across Europe. Our finding of a higher contribution of tree species compared with climatic factors is similar to the work reported by van der Linde et al. (2018), although another study found that the assemblage of fungi at the species level detected using above-ground fruiting bodies and soil DNA sampling was significantly different (Porter et al., 2008). It is worth noting that these two approaches might not be directly comparable if the vast majority of fungi at a site do not produce fruiting bodies. However, we believe that the study based on different sampling methods (i.e., fruiting bodies and DNA sequencing of environmental samples) could be supplemented with each other. An improvement in understanding of the comparability of the two sampling methods will be

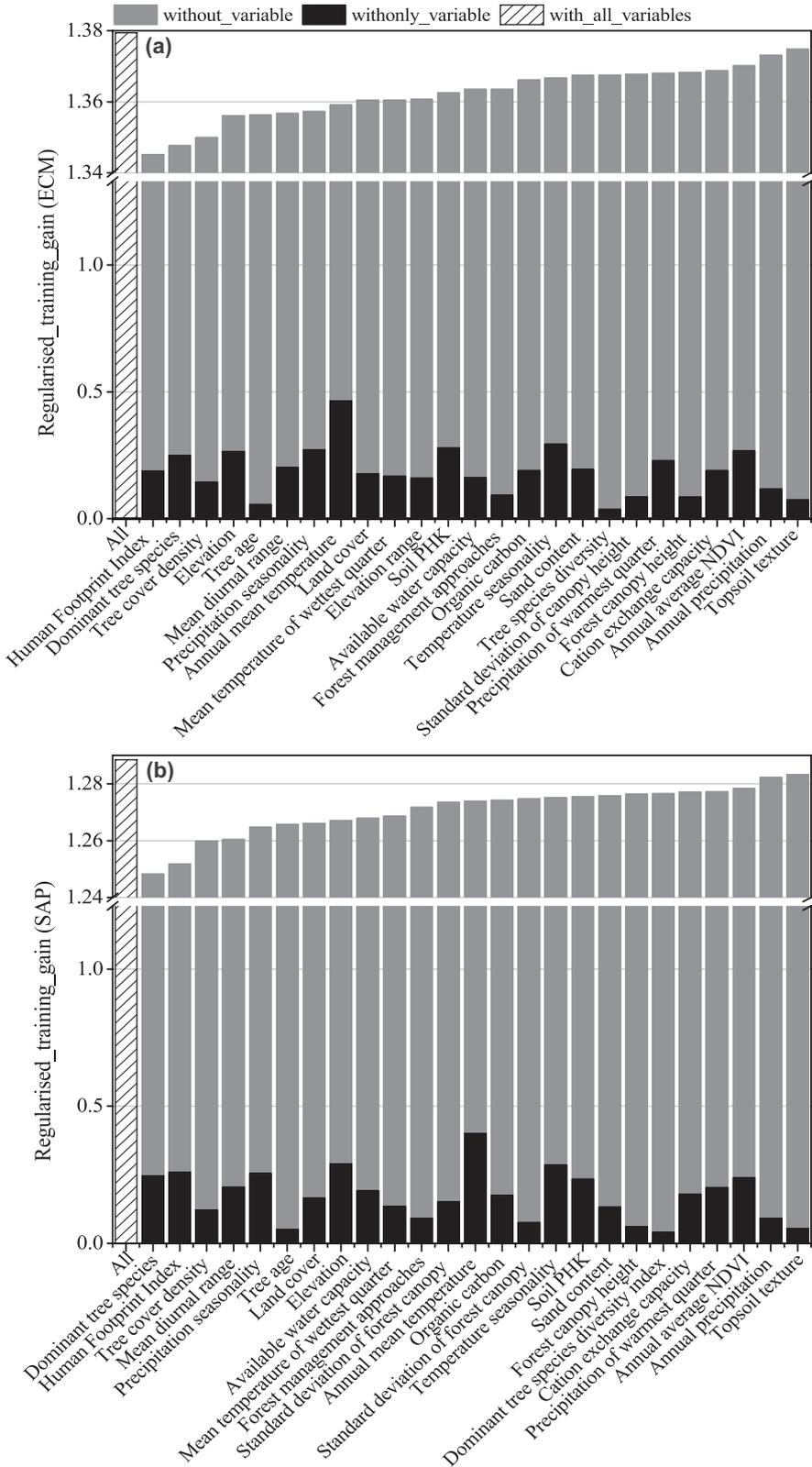


FIGURE 5 The regularized training gain of the model for (a) ectomycorrhizal macrofungi (ECM) and (b) saprotrophic macrofungi (SAP). “with_all_variables” indicates the results of the model when all variables were used. “withonly_variable” indicates the results of the model when a single variable was run in isolation. “without_variable” indicates the effect of removing a specific single variable from the full model

helpful to understand fully the relative importance of host plants and climate in determining the distribution of ectomycorrhizal fungi at large spatial extents.

In compared to ectomycorrhizal fungi, saprotrophic fungi were thought to lack preference for specific tree species in temperate forests (Purahong et al., 2018), and some large-scale studies found no

association between tree species and saprotrophic fungi (Andrew, Buntgen, et al., 2019; Tedersoo et al., 2014). In contrast, we found that the dominant tree species was an important factor influencing the diversity and distribution of saprotrophic macrofungi, which were shown to have a significantly higher distribution probability in areas dominated by *Fagus* spp. and *Picea* spp. than in areas dominated by

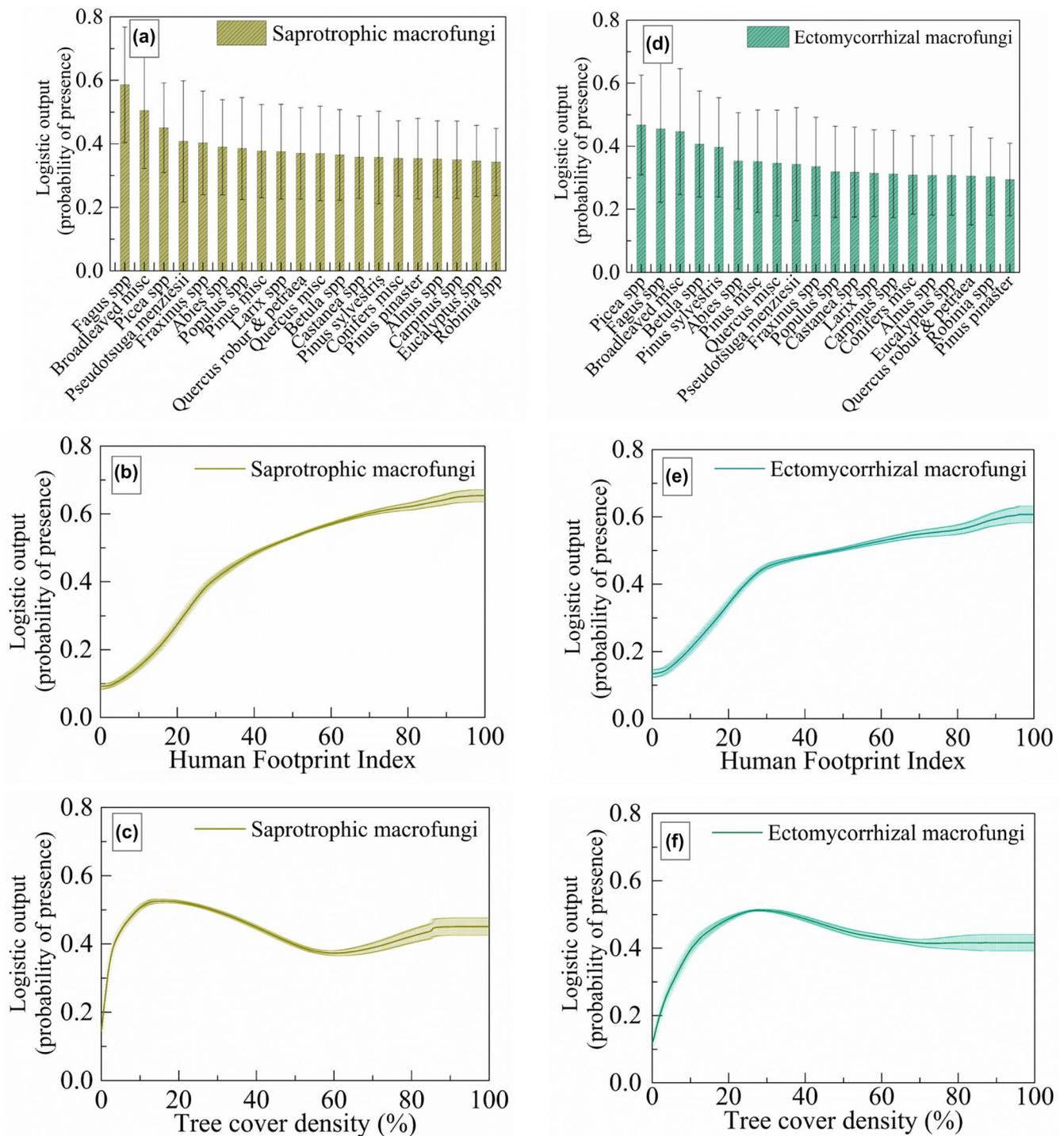


FIGURE 6 The response curve of the distribution probability of (a–c) saprotrophic macrofungi and (d–f) ectomycorrhizal macrofungi to the top three environmental variables. These curves show how the response changed for a particular variable used in isolation. The values show the mean response of all the species in each group and the mean (bar or continuous line) ± 1 SD (whiskers or shaded areas around the mean)

other tree species. Interestingly, studies on saprotrophic fungi at the country level did find beech (*Fagus sylvatica*) to harbour distinctive fungi: Heilmann-Clausen (2003) observed that beech is an important host species for overall wood-inhabiting fungal species richness in Denmark; and Küffer et al. (2008) found the noted richness of saprotrophic fungi in broadleaf forests in Switzerland and Ukraine.

Saprotrophic fungi need to decompose substrate to acquire energy and nutrients, and the amount of available substrate (e.g., dead trees, logs, snags and litter) is important (Bässler et al., 2010; Krahe et al., 2018; Moore et al., 2011). Different tree species have different properties, including the general chemical and structural composition of the wood (Heilmann-Clausen, 2003), and may produce debris

of differing quantity and quality (Purahong et al., 2018), affecting the establishment of saprotrophic fungi. For instance, in deciduous forests, fallen trunks and branches constitute the greater part of dead wood, forming a key habitat for saprotrophic fungi (Boddy et al., 2007). Our results provide further evidence for tree species preference by saprotrophic macrofungi at a large spatial extent.

We note that European forests are dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*), together covering c. 50% of the European Union forest area (Brus et al., 2012). Theoretically, a dominant host is likely to have a stronger selective pressure on the overall species pool (Heilmann-Clausen, 2003). Therefore, the wide distribution of *Picea* spp. and *Fagus* spp., covering a broad range of environmental conditions, might provide high resource availability, providing ecological niches for macrofungi and explaining the importance of European beech and Norway spruce for fungal species richness at a continental level in Europe.

4.2 | Relative importance of human disturbance

For the 25 variables used in our model, the human footprint index contributed significantly to the distribution of ectomycorrhizal macrofungi and saprotrophic macrofungi. We found a positive relationship between the macrofungi distribution probability and the human footprint index. This result is surprising, because several studies have suggested the opposite trend between species diversity and human footprint index (de Thoisy et al., 2010; Giam et al., 2012), and human activity has generally been found to have a negative impact on biodiversity world-wide (Pimm & Raven, 2000). However, widespread changes to species richness as a result of human niche creation are increasingly being discerned (Boivin et al., 2016). The anthropogenic alteration of the landscape often creates novel habitats (Sanderson et al., 2002), thereby increasing the abundance of some naturally rare habitats and benefitting certain groups of fungi (Boddy et al., 2007). For instance, the use of woodchips in horticulture has led to a strong increase in a number of saproxylic fungi (Shaw et al., 2004). Human movement (e.g., hunting or the extraction of resources from the ecosystem) might also provide a mechanism for species dispersal (Sanderson et al., 2002; Walsh et al., 2017), especially for macrofungi, which have a long history of collection and/or cultivation by humans. Areas subject to strong human disturbance (e.g., in and around European urban areas, where a range of ornamental tree and shrub species have become established; Blanus et al., 2019; Kelcey & Müller, 2011) might also provide additional host species for macrofungi. For instance, the introduction of exotic tree species in Danish gardens has been found to have increased the species richness of some groups of fungi (Heilmann-Clausen, 2003). Interestingly, Pautasso (2007) and Pautasso and Chiarucci (2008) found that the positive relationship between human disturbance and species richness was scale dependent. They observed that there was usually a negative correlation between human disturbance and the species richness of plants and vertebrates at the local or landscape

level. However, this correlation became positive as the study scale became coarser. Nevertheless, we cannot rule out the problems of whether there are potentially more observations in areas closer to cities or highly populated areas in our study. Therefore, the relationship between macrofungi and human disturbance at different spatial scales will require further study.

4.3 | Macrofungal diversity and distribution patterns in Europe

Open-access databases provided a large volume of macrofungal observations across an extensive area over a long period. Combined with robust species distribution modelling techniques, presence-only data are adequate to predict habitat suitability and indicate where the species is most likely to occur (Merow et al., 2013). Although these datasets offer the possibility of using predictive models to develop distribution maps (Steen et al., 2019), such data might still be suboptimal compared with carefully designed surveys. For example, there were large differences in the number of macrofungal records held across the eight countries in our study (Supporting Information Appendix S2: Table S2.1); hence, there might be bias in the database owing to differences in sampling level. However, careful data culling provided a potential mechanism for improving predictions from open-access data sources (Steen et al., 2019). Indeed, spatial thinning of species occurrence records and the biased background data sampling method we used in this study will mitigate the possible sampling bias further. There is emerging evidence that SDMs developed using open-source but relatively poorly structured data have the potential to perform as well as those using systematic data (Steen et al., 2019). In a general context, our study using open-access datasets analysed in conjunction with robust SDMs appears useful, especially when alternative data are unavailable.

Our results revealed that eastern Denmark and southern Sweden are likely biodiversity hotspots for both functional groups of macrofungal species. Southern Sweden covers both nemoral and boreonemoral zones (Rydin et al., 1997). The forest in the nemoral zone mainly consists of deciduous broadleaf trees, such as beech and oak, whereas the boreonemoral zone is dominated by either coniferous or broadleaf trees, providing ideal habitats for numerous species, including macrofungi (Nilsson et al., 2001; Nordén et al., 2007). Denmark has also been found to have very high fungal species richness in its beech forest compared with some other European countries (Ódor et al., 2006). There is a relatively large area of old-growth deciduous broadleaf forest in eastern Denmark (Sabatini et al., 2018), which is of key importance to the macrofungal diversity in Europe (Dvořák et al., 2017), because numerous forest fungi have been confined to these old-growth forests according to field observations and red lists (Senn-Irlet et al., 2007). *Fagus* spp. and *Picea* spp., which are important hosts for macrofungi (Küffer et al., 2008; Moore et al., 2011), are widely distributed across eastern Denmark and southern Sweden (Supporting Information Appendix S3: Figure S3.5). Ideal habitat conditions, plus the wide distribution of host tree

species and old-growth forest, are likely to be important reasons for the high diversity of macrofungi in these areas.

4.4 | Conclusions

By taking a group of relatively conspicuous macrofungal species, we investigated the diversity and distribution of two different functional groups of macrofungi at a 5 km spatial resolution at a continental level across eight European countries. We analysed the importance of variables that affect the distribution of macrofungi. Overall, our study demonstrated that tree species and human disturbance played more important roles than climatic factors in determining the diversity and distribution of macrofungi at a continental scale in Europe. Our study indicates that fungal diversity and distribution might change considerably if the strongest predictors (i.e., tree species) are altered by climate change and/or human activity. With changes in fungal diversity, other ecological processes might also be transformed, because fungi are important drivers of ecosystem processes, such as nutrient and carbon cycling.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The datasets used and/or analysed during the present study are available through the GBIF portal (<https://www.gbif.org/>). Download links for specific datasets can be found in Table 1. The R scripts used for the preprocessing of fungal data downloaded from the GBIF are available as Supporting Information (Appendix S2).

ORCID

Haili Yu  <https://orcid.org/0000-0001-9080-1597>

Tiejun Wang  <https://orcid.org/0000-0002-1138-8464>

Andrew Skidmore  <https://orcid.org/0000-0002-7446-8429>

Marco Heurich  <https://orcid.org/0000-0003-0051-2930>

Claus Bässler  <https://orcid.org/0000-0001-8177-8997>

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BIOSKETCH

Haili Yu is a PhD student at the University of Twente. She is interested in biogeography, ecological niche modelling and geographic information system. Her current research focuses on diversity and distribution patterns of macrofungi, and she seeks to understand the factors and processes causing these patterns at multiple geographical scales.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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