

How future climate and tree distribution changes shape the biodiversity of macrofungi across Europe

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Abstract

Aim: Climate change is affecting biodiversity at an accelerating rate. Despite the importance of fungi in ecosystems in general, and in the global carbon and nitrogen cycle in particular, there is little research on the response of fungi to climate change compared with plants and animals. Earlier studies show that climatic factors and tree species are key determinants of macrofungal diversity and distribution at large spatial scales. However, our knowledge of how climate change will affect macrofungal diversity and distribution in the future remains poorly understood.

Location: Europe.

Methods: Using openly available occurrence data of 1845 macrofungal species from eight European countries (i.e. Norway, Sweden, Finland, Denmark, Netherlands, Germany, France and Spain), we built ensemble species distribution models to predict macrofungal response to climate change alone and combined climate and tree distribution change under the IPCC special report on 2080 emissions scenarios (SRES A2 and B2).

Results: Considering climate change alone, we predict that about 77% (74.1%–80.7%) of the modelled species will expand their distribution range, and around 57% (56.1%–58.4%) of the modelled area will have an increase in macrofungal species richness. However, when considering the combined climate and tree species distribution change, only 50% (50%–50.9%) of the species are predicted to expand their distribution range and 49% (47.4%–51.1%) of the modelled area will experience an increase in macrofungal species richness.

Main Conclusions: Overall, our models projected that large areas would exhibit increased macrofungal species richness under future climate change. However, tree species distribution might play a restrictive role in the future distributional shifts of macrofungi. In addition, macrofungal responses appear heterogeneous, varying among species and regions. Our findings highlight the importance of including tree species in the projection of climate change impacts on the macrofungal diversity and distribution on a continental scale.

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KEYWORDS

biogeographical region, ensemble species distribution model, range shift, range size, scenarios, species turnover rate

1 | INTRODUCTION

Ongoing climate change is affecting the phenology and distribution of various organisms worldwide (Parmesan, 2006; Pecl et al., 2017), and it has been identified as a major threat to global biodiversity in the coming decades (Bellard et al., 2012; Gomes et al., 2019; Román-Palacios & Wiens, 2020; Smale et al., 2019). However, compared with plants and animals, there is limited research on fungal responses to climate change, despite their importance in the global carbon and nitrogen cycle (Mueller & Schmit, 2007).

Fungi are a major component of almost all terrestrial ecosystems on Earth (Moore et al., 2011). As a distinct kingdom, fungi form a large and diverse group of species and play a vital role in carbon storage and nutrient cycling (Blackwell, 2011; Mueller & Schmit, 2007; Tedersoo et al., 2014). The two main functional groups in the fungi kingdom that participate in regulating global carbon and nutrient cycles are mycorrhizal fungi and saprotrophic fungi (Baldrian et al., 2022; Dighton, 2016). Mycorrhizal fungi (such as arbuscular mycorrhizal fungi, ectomycorrhizal fungi and ericoid mycorrhiza) form mutualistic relationships with plants, whereby fungi can obtain carbon (photosynthate) from their host plants while transferring nutrients (e.g. nitrogen and phosphorus) to their host (Watkinson et al., 2015). These mutualistic relationships could increase the potential of plants to sequester CO₂ from the atmosphere into soils (Soudzilovskaia et al., 2019; Terrer et al., 2016). Unlike mycorrhizal fungi, saprotrophic fungi support the global nutrient cycle and contribute to the carbon cycle by absorbing nutrients from dead organic matter (Dighton, 2016). Thus, fungi play an essential role in regulating the global carbon cycle, which is closely linked to climate change (Battin et al., 2009). However, our knowledge of how climate change will affect the diversity and distribution of fungi in the future remains poorly understood.

Most fungi live in substrates or underground, so it can be difficult to directly observe their response to climate change in the field, especially on a large spatial scale. However, there is a large group of fungi that produce visible fruiting bodies (hereafter macrofungi) above ground (Mueller & Schmit, 2007), which are useful for recording fungal presence and investigating the fungal response to the environment (Heegaard et al., 2017; Wollan et al., 2008). Especially among the class Agaricomycetes, which is one of the largest and most conspicuous groups of fungi, there is a great diversity in fruiting body forms and nutritional modes related to the carbon and nitrogen cycle (e.g. ectomycorrhizal and saprotrophic macrofungi; Sánchez-García et al., 2020). Past studies have reported that climate change is already impacting macrofungal reproduction, distribution and physiology (Willis, 2018). For example, the timing of

macrofungi fruiting has been found to be sensitive to climate and has changed over the last century (Diez et al., 2013; Gange et al., 2007; Kausrud et al., 2008, 2012); the fruiting patterns of many fungal species in the Alps exhibited altitudinal upwards shifts between 1960 and 2010 (Diez et al., 2020). But few studies predicted change in macrofungal diversity and distribution in future climate change scenarios. Nevertheless, understanding fungal responses to climate change is important for forecasting future ecosystem changes (Diez et al., 2013).

Many earlier studies on other species tend to focus solely on the impacts of climate change (Bellard et al., 2012; Sirami et al., 2017; Yu, Wu, et al., 2021). However, macrofungi are affected by climate directly or indirectly by the effects of climate on the organisms with which they are associated (Vitasse et al., 2021). As outlined above, plants provide carbon to macrofungi (Bässler et al., 2010; Krahe et al., 2018; Watkinson et al., 2015), and many local studies have found that macrofungi composition and diversity are affected by the tree species composition and diversity (Jaroszewicz et al., 2021; Schmit et al., 2005; Zhang et al., 2010). A recent study also revealed that the dominant tree species play a crucial role in determining the diversity and distribution of macrofungi at the continental scale (Yu, Wang, et al., 2021). Given that tree species can form mutualistic relationships with macrofungi and provide them with resources, potential changes in tree species diversity and distribution under ongoing climate change (Lenoir et al., 2008; Vitasse et al., 2021) are likely to further influence related macrofungal diversity and distribution. Thus, we hypothesize that the macrofungal response to climate change alone and the combined changes in climate and tree species distribution in the future might be different.

Disentangling the effects of climate change and tree species distribution change on macrofungal diversity and distribution is essential to reveal the biological consequences of diverse climate change scenarios. Here, using openly available occurrence data of 1845 macrofungal species from eight European countries (i.e. Norway, Sweden, Finland, Denmark, Netherlands, Germany, France and Spain), we build ensemble species distribution models for current and future conditions, to investigate the response of macrofungi to climate change alone and climate change in combination with changes in tree species distribution, under the Intergovernmental Panel on Climate Change (IPCC) special report on emissions scenarios (SRES: A2 and B2) in 2080. We investigate species range change (gains and losses of suitable habitat), as well as predicted changes in fungal species richness across biogeographical regions, spatial patterns of turnover rate and the projected spatial shift of macrofungal species. Therefore, we provide new insights into macrofungal responses to changing climate and tree species distributions in Europe.

2 | METHODS

2.1 | Occurrence data of macrofungal species

We downloaded fungi data from the Global Biodiversity Information Facility (GBIF; <http://data.gbif.org>), which gathers species records from various sources worldwide and is currently the largest species occurrence observations database (Chandler et al., 2017; Hochmair et al., 2020). GBIF defines standards for publishing data and performs additional checks to verify data quality. It contains long-term investment information in biological science and is an essential source of species occurrence (Elith et al., 2011).

For our study, we extracted georeferenced fungal occurrence records collected between 1990 and 2018 from eight European countries: Norway, Sweden, Denmark, Netherlands, Finland, Germany, France and Spain (GBIF.org, 2022). These countries contained a relatively large amount of fungal occurrence data that were contributed by various organizations (e.g. university projects, biodiversity centres and mycological societies) to GBIF. We filtered out macrofungal species records from seven orders under Agaricomycetes, namely the *Agaricales*, *Boletales*, *Cantharellales*, *Hymenochaetales*, *Polyporales*, *Russulales* and *Thelephorales*, for our further study.

Since most of the macrofungal species records downloaded from the GBIF data portal have a spatial resolution (coordinate uncertainty) of 5 km, we chose a 5 km grid size for our study. All macrofungal occurrence data were placed in 5 × 5 km grids, which we generated based on European Terrestrial Reference System 1989 (ETRS89) datum and Lambert Azimuthal Equal 176 Area (LAEA) projection (EPSG: 3035) across our study area. In order to improve the data usability and consistency, we screened the macrofungal data and only retained records that included the specific species name and disregarded records flagged with taxonomic issues. As the grid size used in our study is 5 × 5 km, we removed the records with a 'coordinate uncertainty' larger than 5 km. We rarefied records spatially by eliminating all but one point present per species within each 5 × 5 km grid cell, to avoid double counting the presence of each species and to reduce overfitting to sampling bias in species distribution models. Furthermore, we removed species recorded in <30 grid cells to safeguard the validity of the predictive performance of the species distribution models and ensure access to a reasonable number of test data for modelling (Wisz et al., 2008).

In total, we compiled a dataset with 1845 macrofungal species and 878,978 records for final use in our model (Figure 1). More details of the dataset can be found in the study of Yu, Wang, et al. (2021). All statistical analyses reported in this study, including the preprocessing of fungi data and predictor variables, were conducted in R (R Core Team, 2013).

2.2 | Predictor variables

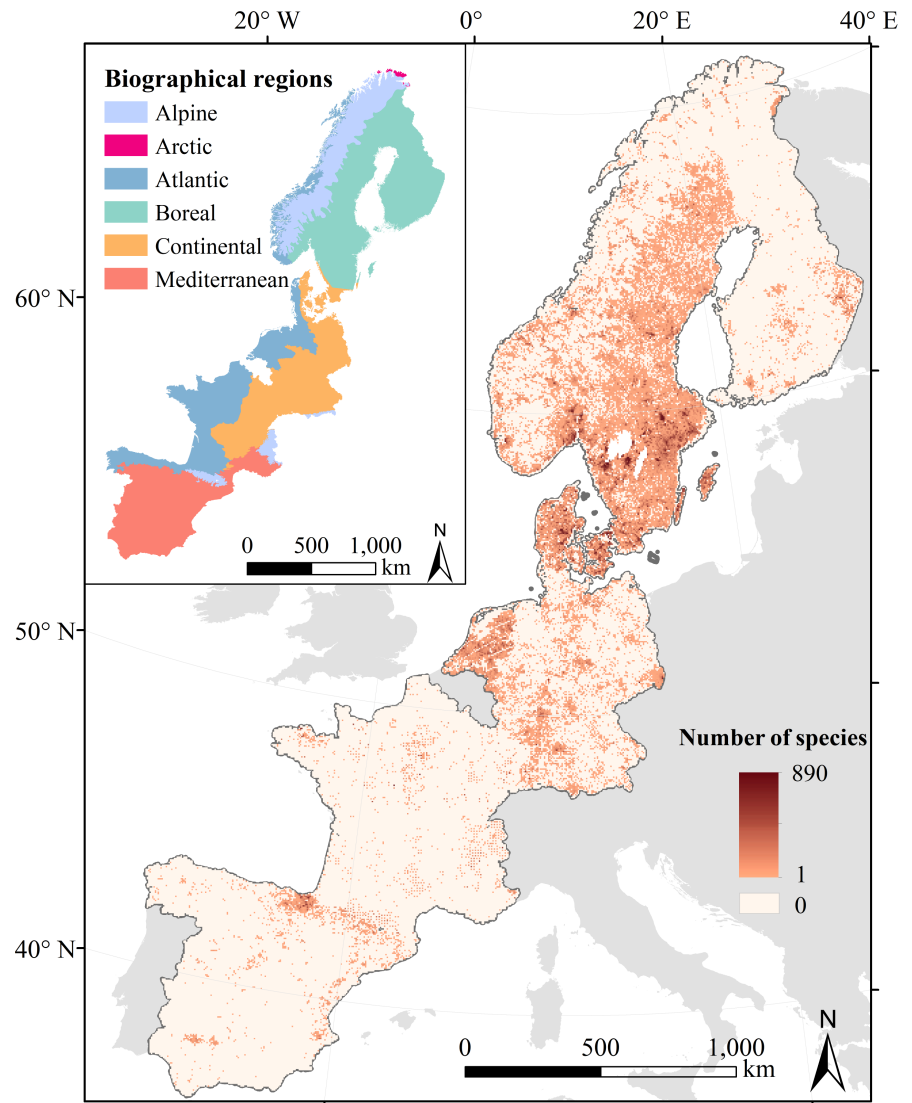
2.2.1 | Climate

Our study used bioclimatic variables derived from monthly climate to highlight climate conditions best related to species physiology, such as annual trends, intra-year seasonality and stressful conditions influencing species niches (Fick & Hijmans, 2017; O'Donnell & Ignizio, 2012). We obtained 19 bioclimatic variables for current (<https://www.worldclim.org/>, Fick & Hijmans, 2017) and future conditions (http://www.ccafs-climate.org/data_spatial_downscaling/, Navarro-Racines et al., 2020) at a spatial resolution of 2.5 arc minutes (~5 km). To ensure consistency with future tree species distribution scenarios used in this study, we selected the future climatic factors that were calculated based on monthly climate under the IPCC (2001) Special Report on Emissions Scenarios storyline (SRES) A2 and B2 for 2080. A2 describes high energy requirements with a high rate of population growth and land-use change, while B2 describes a comparatively less heterogeneous future world with lower energy requirements and population growth and land-use change (IPCC, 2001). For each scenario, the value of each bioclimatic variable was the average of three General Circulation Models (GCMs), i.e. CCCMA CGCM2, CSIRO MK2 and HCCPR_HADCM3.

2.2.2 | Tree species

We took three variables related to tree species composition and diversity into account. These were dominant tree species, tree species richness and Simpson's Index of Diversity (1 - D) in each 5 × 5 km grid according to previous fungal studies (Spake et al., 2016; Van Der Linde et al., 2018; Wollan et al., 2008; Yu, Wang, et al., 2021). These variables were calculated based on modelled distribution maps of 28 tree species in Europe for the current and two future scenarios (SRES A2 and B2) in 2080 with a resolution of 1 km, which were obtained from the European Commission (Casalegno et al., 2009, see all download links in Table S1). The distributions of these 28 tree species for both current and future climate were modelled using the Random Forest ensemble classifier based on the Forest Focus European dataset of species presence/absence, bioclimatic and other ecological data (Casalegno et al., 2010, more details can be found on the data description page, see Table S1). These tree species covered the most ecologically important and spatially most abundant tree species in the European forests, which is representative of the forests in our study area (Buras & Menzel, 2019). For each scenario (current, SRES A2 in 2080s and SRES B2 in 2080s), we calculated the dominant tree species by choosing the species with maximum coverage in each 5 km grid from the distribution maps of the 28

FIGURE 1 Spatial distribution of the number of macrofungal species sampled per 5 × 5 km grid cell and six biogeographical regions in the study area.



tree species. Additionally, we calculated the species richness and Simpson's Index of Diversity ($1 - D$) for the 5 km grid using the 'vegan' package (Dixon, 2003).

Multicollinearity is a problem because it distorts the statistical significance of the independent variable (Dormann et al., 2013). To avoid multicollinearity, we calculated the variance inflation factor (VIF, Akinwande et al., 2015) for all predictor variables using the 'vifstep' function from the 'usdm' package (Naimi, 2015). We excluded one variable with the highest VIF, then repeated the procedure until there were no variables with a VIF greater than 5 (Akinwande et al., 2015; Větrovský et al., 2019). The final predictor variables used in our models included six bioclimatic variables (Bio02—mean diurnal temperature range (°C); Bio04—temperature seasonality (°C); Bio08—mean temperature of wettest quarter (°C); Bio15—precipitation seasonality (coefficient of variation); and Bio18—precipitation of warmest quarter (mm)) and three tree species related variables (dominant tree species, richness of tree species and Simpson's Index of tree species).

To investigate how future tree distribution change might affect macrofungi diversity and distribution, we ran our species

distribution models with two sets: (1) climate change alone, using the future climatic variables in 2080 but current dominant tree species and their richness and Simpson's Index of diversity as predictors, (2) combined climate and tree distribution change, using both future climatic variables and future dominant tree species and their richness and Simpson's index of diversity in 2080 as predictors (Figure S1).

2.3 | Ensemble species distribution models

Multiple species distribution models (SDMs) have been proposed in the past two decades and applied to mycology (Hao et al., 2020); however, the performance of different techniques can vary significantly (Elith et al., 2006). To reduce model uncertainty and improve the predictive power of SDMs, the ensemble approach that combines different SDM algorithms has been widely used (Araújo & New, 2007; Naimi & Araújo, 2016a, 2016b; Thuiller et al., 2009). Thus, we predicted the probability of macrofungi occurrence using an ensemble modelling approach combining four different species distribution model methods using the 'sdm' package (Naimi &

Araujo, 2016a, 2016b). We selected one classic and widely used regression-based method, generalized linear models (McCullagh & Nelder, 2019) and three high-performance machine learning methods (Elith et al., 2006), random forests (Breiman, 2001), boosted regression trees (Friedman, 2001) and MaxEnt (Phillips et al., 2006). We applied these four methods with default settings in the 'sdm' package to avoid an overwhelming complexity (Naimi & Araujo, 2016a, 2016b).

2.3.1 | Biased pseudo-absence data

As our macrofungal data are presence-only data, additional data representing the range of environmental conditions (known as pseudo-absence data, which contrasts against the presence locations) in the modelled region is needed to run the species distribution models (Barbet-Massin et al., 2012). Usually, these pseudo-absence data are generated randomly across the study area; however, occurrence data are often thought to be spatially biased towards easily accessible areas. Thus, these differences between the distribution of occurrence and random pseudo-absence sampling could lead to inaccurate models (Phillips et al., 2009). To alleviate this potential bias, we selected the pseudo-absence sample that reflects the same bias as the presence data (Kramer-Schadt et al., 2013; Namyatova, 2020; Phillips et al., 2009) by producing a sampling probability surface, with which the cell values reflect the sampling effort and give weight to choosing pseudo-absence data (Fourcade et al., 2014). We created the bias surface by mapping a two-dimensional Gaussian kernel density (Elith et al., 2010; Fourcade et al., 2014) on the extent of the modelled area based on the species occurrence distribution with the 'kde2d' function from the 'MASS' package (Ripley et al., 2013). Then, we sampled 10,000 (Barbet-Massin et al., 2012) biased points according to the bias surface to generate 'pseudo-absence' data for each species. Due to the limited knowledge of fungal dispersal ability, our study assumed that fungal species are not dispersal limited at the scale of our study. Thus, we sampled the 'pseudo-absence' data across the entire study area.

2.3.2 | Block cross-validation method

The model validation was performed using spatial cross-validation procedures. Cross-validation is commonly used to evaluate model performance when no independent data are available. It partitions the data into k folds, using one fold to test and the remaining ($k - 1$ folds) for model fitting (Hastie et al., 2009; Valavi et al., 2019). Usually, the data are randomly split into different folds; however, when the folds are split strategically (temporal or spatial strategy is used) rather than randomly, it is called block cross-validation (Roberts et al., 2017).

Ecological data are often autocorrelated in space or time (Dormann et al., 2013), and random splitting of data might not guarantee spatial independence and may overestimate model

performance (Roberts et al., 2017; Valavi et al., 2019). The block cross-validation, which splits the training and test datasets in a spatially separated manner, helps to test whether the model performs as well in the distant locations from the training data area as it does in the more adjacent area and is recommended for assessing model transferability (Roberts et al., 2017; Valavi et al., 2019). In particular, block cross-validation can be useful for assessing models aiming to predict new climatic conditions (Valavi et al., 2019).

Due to the study area covering a wide range of latitudes, we split both presence and 'pseudo-absence' data into geographically nonoverlapping horizontal bins (blocks) along the latitude. We then distributed these blocks into five spatially separated folds. We produced these folds using the 'blockCV' package (Valavi et al., 2021). Presence and 'pseudo-absence' data within the same fold were used together. For each run of each species and each method, four folds (80% of the dataset) were randomly selected to train the model, and the remaining one fold (20% of the dataset) was used to test the model. We repeated the procedure five times (5-fold cross-validation) until each fold of the five folds was used as the testing fold. In total, we ran 20 models for each species.

2.3.3 | Model performance evaluation

We calculated the area under the receiver-operating characteristic curve (AUC) and true skill statistics (TSS; Allouche et al., 2006) to evaluate the model performance based on block cross-validation. AUC is a threshold-independent method, ranging from 0 to 1, where 1 indicates perfect discrimination (Swets, 1988). Although criticized, the AUC is a standard method for measuring prediction accuracy and is widely used in ecological studies (Elith et al., 2006; Phillips et al., 2006). True skill statistics is a frequently used threshold-dependent method, which is an intuitive measure of the performance of species distribution models when predictions are expressed as presence-absence maps (Allouche et al., 2006). True skill statistics scores range from -1 to 1 , where 1 indicates perfect agreement and values of zero or less indicate a model that performs no better than random, with a value greater than 0.5 widely used to indicate good model performance (Hill et al., 2017; McGinty et al., 2021; Tanaka et al., 2020). For our study, we excluded models with a TSS value lower than 0.5 and used the remaining models with good performance (i.e. TSS value ≥ 0.5) to create the ensemble projection. The ensemble projection was created in the 'sdm' package (Naimi & Araujo, 2016a, 2016b) based on the weighted mean of the four algorithm projections using TSS scores as a weighting factor.

2.3.4 | Binary conversion of model outputs

The default output of SDMs is a continuous value ranging from 0 to 1, with high values indicating high suitability. To produce the species diversity map for macrofungi, we transformed the model output into binary (presence/absence) predictions using the maximum of

the sum of specificity (quantifying commission errors) and sensitivity (quantifying omission errors; Max SSS) as a threshold for each species. The Max SSS threshold minimizes the error rate of both commission and omission errors and has been widely used in species distribution models (Adam et al., 2021; Fourcade et al., 2018; Liu et al., 2013; Vincent et al., 2019).

2.4 | Analysis of predicted macrofungal responses

To quantify the response of macrofungi to future climate and tree distribution change, we estimated the projected range changes (including species range size, gain or loss of suitable habitat area) for each species, calculated the change of species richness and species turnover rate and explored species range shifts direction and distance. We further analysed the differences in these changes among the nine biogeographical regions (Roekaerts, 2002) in our study area. Biogeographical regions are geographical areas defined by the distinct assemblages of species and communities found in them, constituting a cornerstone for ecology, biogeography, evolution and conservation biology (Roekaerts, 2002; Sundseth & Barova, 2009).

2.4.1 | Predicted change in species richness and turnover rate

We summed up the binary outcome of species presence for each grid cell to yield species richness of macrofungi in the current scenario and two future model scenarios. We then calculated the difference between species richness in the two future model scenarios relative to the current species richness, respectively.

To evaluate the turnover rate of macrofungal species in the study area, we summed the number of species lost (Ls) and gained (Gs) relative to the current species richness in each pixel. Then, for each pixel, the percentage of species turnover is given by $100 \times (Gs + Ls) / (Gs + SR)$, where SR is the current species richness (Thuiller et al., 2005). This equation obtained the fraction of the sum of extinctions and immigrations to the total number of species across both current and future scenarios, and it is the simplest and widely used way to quantify species composition change (Hillebrand et al., 2018). To further explore the spatial change of macrofungi diversity, we calculated the area proportion of species richness that increased, decreased and unchanged in each biogeographical region and the mean turnover rate of each biogeographical region in the study area. To highlight any geographical inconsistency in predicting the potential impact of climate change from different modelling methods, we calculated the standard error of the predicted species richness change and turnover rate of the four individual methods for each scenario.

2.4.2 | Predicted change in species range size

We calculated species range size based on the number of grid cells of suitable habitat for each species. We summed the number of pixels gained (G, newly suitable grid cells), pixels lost (L, loss of currently suitable grid cells) and pixels stable (S, stable suitable grid cells in future) by each species for different future scenarios. Gain of newly suitable habitat area (%) is given by $100 \times G / (L + S)$, loss of currently suitable habitat area (%) is given by $100 \times L / (L + S)$, and species range change (%) is given by $100 \times (G - L) / (L + S)$ (Thuiller et al., 2009).

2.4.3 | Predicted species range shift

We estimated the projected spatial shift direction and magnitude (distance) of macrofungi distribution based on species range centroid (geometric centre of species range) between current and future binary SDMs using SDMToolbox 2.0 (Brown, 2014).

3 | RESULTS

3.1 | Model performance

The ensemble species distribution models for macrofungi performed well, with a mean AUC of 0.85 (± 0.06 SD) and a mean TSS of 0.64 (± 0.11 SD). Overall, both MaxEnt and random forest had a significantly higher AUC than other methods, and MaxEnt also had a significantly higher TSS than other methods (Table S2, Kruskal–Wallis rank sum test; $p < .001$).

3.2 | Macrofungal species range change

Overall, we predicted that more than half of the species in our study area would have an increased species range size under both climate change alone (80.7% for SRES A2 and 74.1% for SRES B2; Figure 2) and combined climate and tree distribution change (50% for SRES A2, 51% for SRES B2; Figure 2). However, compared with the climate change alone scenario, more species (565 species for SRES A2 and 415 species for SRES B2; Figure 2) were predicted to decrease range size under combined climate and tree distribution change.

At the species level, we predicted that 58.4% (under the SRES A2 scenario, Figure 3a) and 34.2% (under the SRES B2 scenario, Figure 3c) of the species would have a reduced area of newly suitable habitat under the combined effect of climate and tree distribution change in the eight countries. Meanwhile, more than 90% of the species were predicted to have more loss of currently suitable habitat area under the combined climate and tree distribution change scenario (Figure 3b,d).

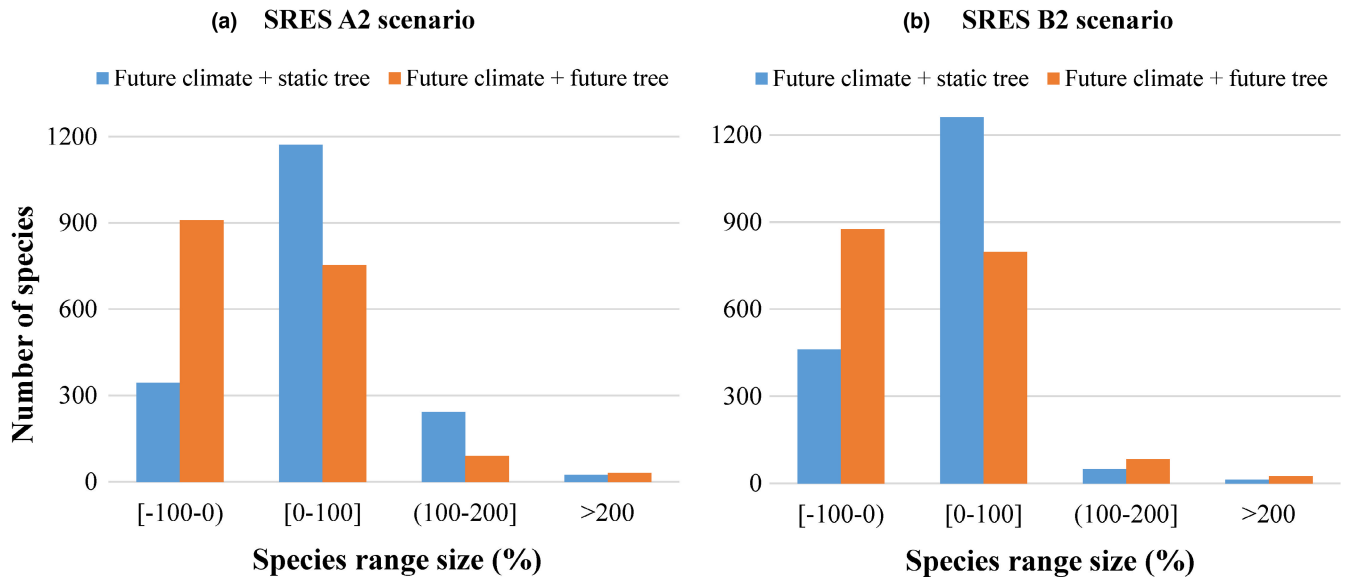


FIGURE 2 Number of species in each class of species range change for macrofungi under climate change alone (light green) and under combined climate and tree distribution change (green) for SRES A2 scenario (a) and SRES B2 scenario (b) in 2080. For each species: Species range change = (Range size in 2080 – Current range size)/Current range size \times 100.

3.3 | Macrofungal species richness change and turnover

Under climate change alone, we predicted that 58.4% (under SRES A2 scenario, Figure 4a) and 56.1% (under SRES B2 scenario, Figure 4c) of the study area showed increased species richness. However, when considering the future combined climate and tree distribution change, the percentage reduced to 47.4% (under SRES A2, Figure 4b) and 51.1% (under SRES B2, Figure 4d).

There is a variation in species richness change among different biogeographical regions. Under climate change alone, more than half of the area in the Mediterranean biogeographical region (64.6% for SRES A2 and 54.1% for SRES B2, Figure 5) was predicted to show decreased species richness, while in all the other regions, most areas (>50%) were predicted to show increased species richness. However, under combined climate and tree distribution change, most areas in both Atlantic biogeographical regions (61.4% for SRES A2 and 60.0% for SRES B2, Figure 5) and Mediterranean biogeographical regions (72.6% for SRES A2 and 64.1% for SRES B2, Figure 5) were predicted to have decreased species richness.

Overall, we predicted a high turnover rate in our study area under future climate change. The mean turnover rate under climate change alone was 70.1% for SRES A2 scenario and 63.8% for SRES B2 scenario, while under combined climate and tree distribution change was 84.8% for SRES A2 scenario and 81.0% for SRES B2 scenario (Figure 6). The Boreal biogeographical region had the highest turnover rate (Figure 7). Compared with climate change alone, the combined climate and tree distribution change predicted a higher turnover rate in most areas (Figures 6 and 7).

3.4 | Macrofungal species distribution shift

Most macrofungal species were predicted to shift to the northeast of our study area under future climate change (Figure 8). Compared with climate change alone, the combined climate change and tree distribution change would cause more species to shift towards the north or the northeast direction (Figure 8).

4 | DISCUSSION

4.1 | Restrictive effects of tree species on the shift of macrofungi

Our findings indicate that tree species distribution may play a restrictive role in the future distribution of macrofungi and the amount of suitable habitat. Under combined climate and tree distribution change, we predicted that in our study area, about half of the modelled species would gain less suitable habitat. Concurrently, more than 90% of the species would have more loss of their currently suitable habitat. It should be noted that our exploratory analysis also showed that the two different functional groups of macrofungi (i.e. ectomycorrhizal and saprotrophic macrofungi) did not have evident differences in their response to future climate and tree distribution changes (Figure S2). These findings indicate that even if the climate is favourable for a fungal species, it cannot grow in the absence of suitable tree species (Guo et al., 2017). However, ectomycorrhizal fungi exhibit different preferences for tree species. For example, Yu, Wang, et al. (2021) found that there was a significantly higher

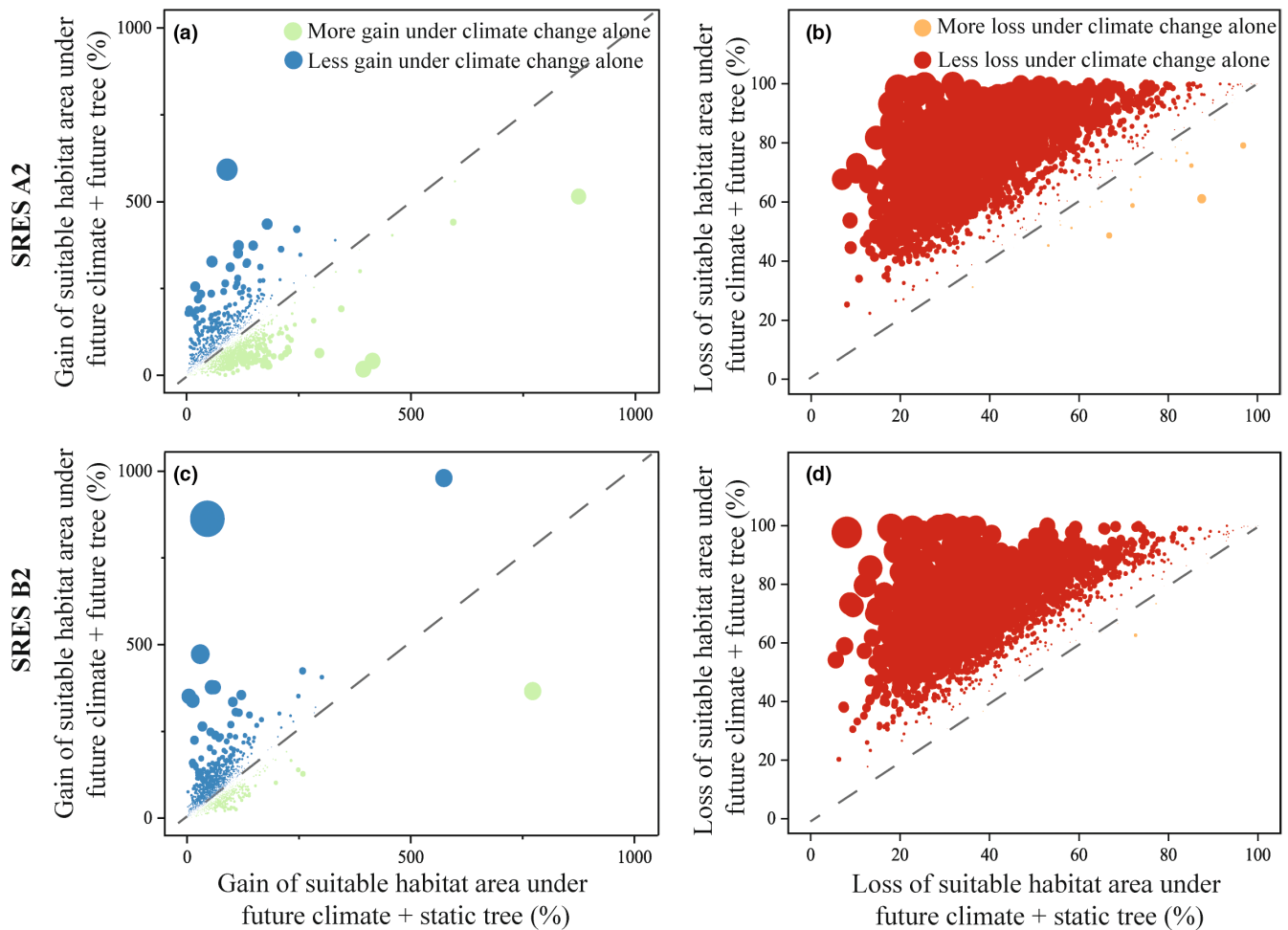


FIGURE 3 Comparison of change of macrofungi suitable habitat area under climate change alone and under combined climate and tree distribution change for two scenarios in 2080. Gain of suitable habitat area under climate change alone and under combined climate and tree distribution change for SRES A2 scenario (a) and SRES B2 scenario (c); Loss of suitable habitat area under climate change alone and under combined climate and tree distribution change for SRES A2 scenario (b) and SRES B2 scenario (d). Each dot represents the value of one species under two situations, with the size of that dot proportional to the difference between the two values. The equal projection line (dashed line 0,0 to 1500,1500 in [(a) and (c)] and dashed line 0, 0 to 100, 100 in [(b) and (d)]) represents the point at which the two projections are equal. The green and orange colours indicate points below the equal projection line; the blue and red colours indicate points above the equal projection line. Gain of habitat represents the percentage of newly occupied sites to the species' current distribution size, while loss of habitat represents the percentage of currently occupied sites to be lost to the species' current distribution size.

distribution probability of ectomycorrhizal fungi in *Picea* spp. and *Fagus* spp. dominated areas than in areas dominated by other tree species. In addition, different tree species can have various chemical properties or structural compositions of their leaf and wood, which would affect the resource (substrate) for saprotrophic fungi (Bässler et al., 2010; Krah et al., 2018). Thus, fungi might disappear from or not expand into climatically suitable areas without suitable tree species.

The response of macrofungi to tree species distribution change is species-specific and varies among regions. In our study area, some macrofungal species have been predicted to gain more suitable habitats because of the change in tree distribution (Figure S3a–d). Some would lose more suitable habitats (Figure S3m–p), and some have not shown much difference between changes under climate

change alone and under the combined climate and tree distribution change (Figure S3i–l). Given such a large number of species (1845) will occupy different habitats and contain different host (e.g. tree species) preferences, the species-specific response of macrofungi to tree distribution change is to be expected. In terms of variation across regions, more Alpine and Arctic biogeographical areas are expected to exhibit increased macrofungal richness under the combined changes in climate and tree distribution. We found that only these two regions are predicted to have increased tree species richness and diversity in the future (Figure S4). A high richness and diversity of tree species could offer opportunities for a wide range of macrofungal species to establish symbiotic relationships and provide the macrofungi with habitat and various resources.

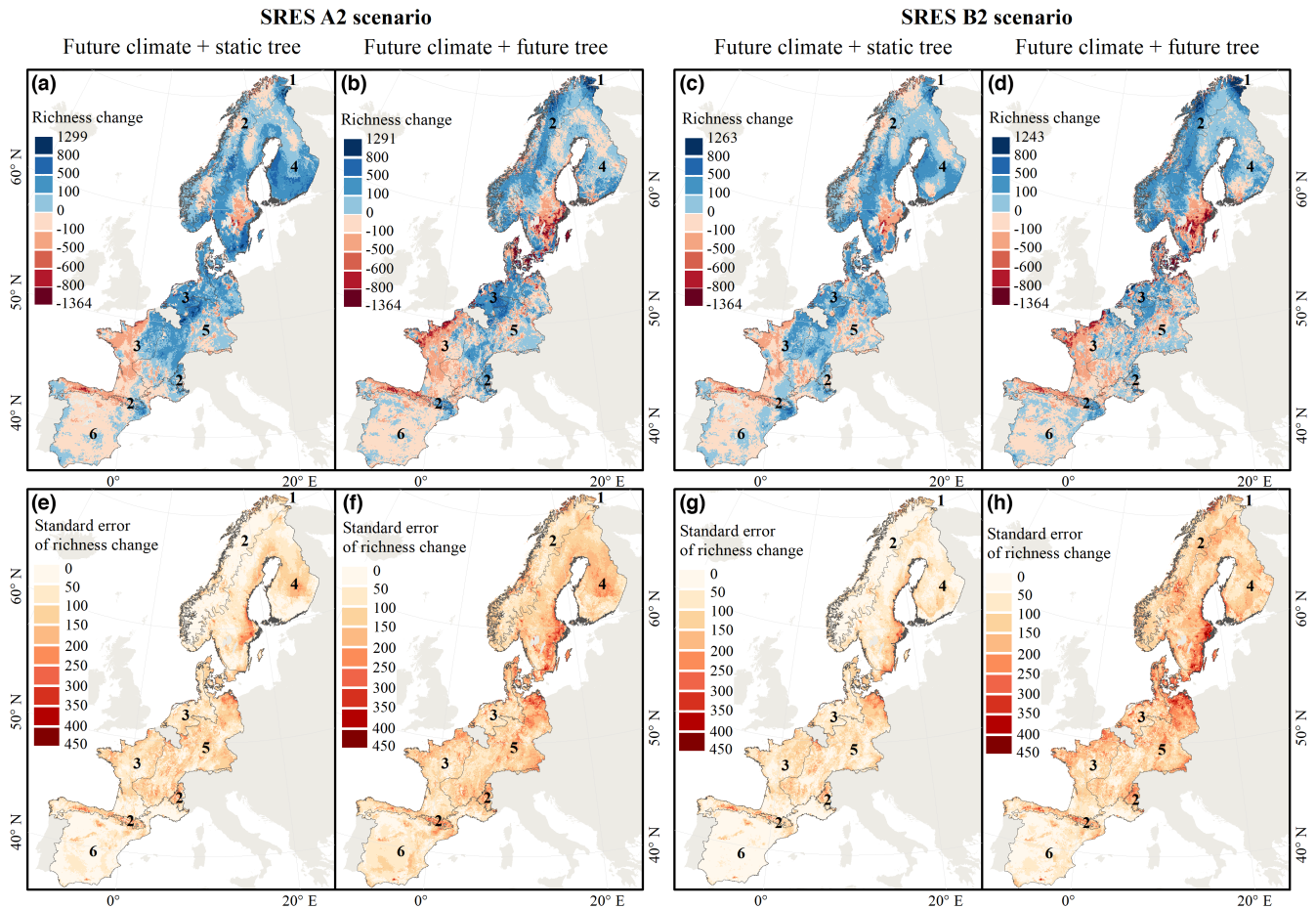


FIGURE 4 Spatial pattern of changes in macrofungi species richness (a–d) and the standard errors of the changes calculated across methods (e–h) under climate change alone (a, c, e and g) and under combined climate and tree distribution change (b, d, f and h) for SRES A2 (a, b and e, f) and SRES B2 (c, d and g, h) in 2080. The number on the study area map shows the biogeographical regions in the study area: 1 Arctic, 2 Alpine, 3 Atlantic, 4 Boreal, 5 Continental and 6 Mediterranean.

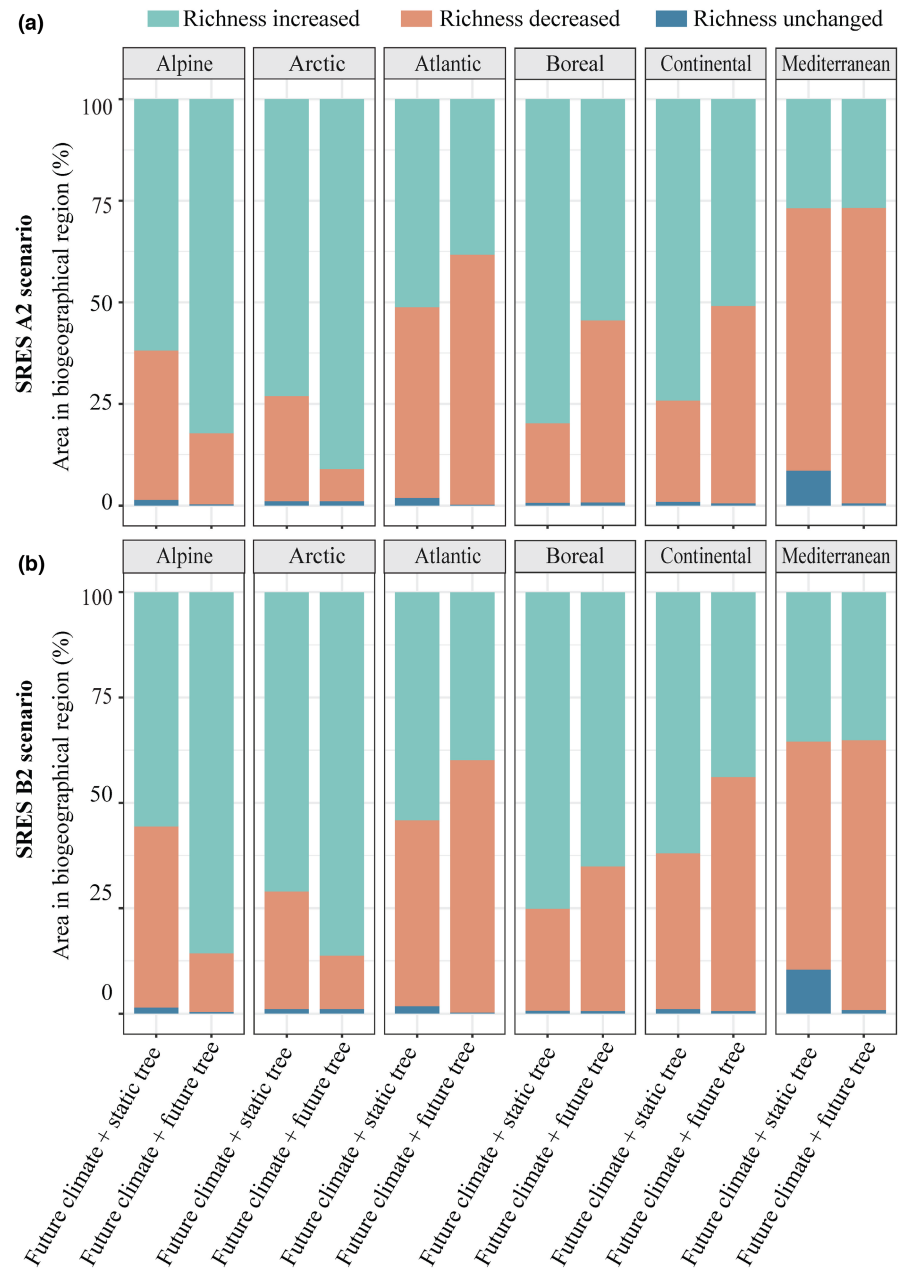
4.2 | Macrofungal species response to future climate change

Our models predicted that large areas of the study area would show increased species richness under future climate change. More than half of the studied macrofungal species were predicted to have a larger suitable habitat, though the other several hundred macrofungal species were predicted to experience contractions of their suitable habitat. Most macrofungal species were predicted to shift to the northeast of our study area under future climate change. Our predictions of the increased richness in many areas and the distributional shifts of macrofungi under future climate change are in line with some findings based on long-term field observations under changing climate in the past. For example, a long-term fungal inventory provided evidence for a significant increase in mushroom productivity and an approximate doubling in the number of fungal fruiting bodies in Switzerland under changing climate (Büntgen et al., 2012). Another study based on 50 years of historical fungal fruit body records in the European Alps found that many macrofungal species showed altitudinal upward shifts (Diez et al., 2020). Some autumnal fruiting species in southern England were found fruiting twice a year (both

in spring and autumn) under climate warming (Gange et al., 2007). Additionally, some studies on future climate change also predicted increased suitable habitats for some specific macrofungal species in different regions (Čejka et al., 2020; Guo et al., 2019; Shrestha & Bawa, 2014).

Compared with the studies at the local scale, our modelled responses of macrofungal species over a large spatial extent showed variation among different biogeographical regions. Overall, our results showed that the Atlantic, Mediterranean and Continental biogeographical areas would suffer a higher macrofungal species richness decrease than other regions. The projected climate change varies among biogeographical regions in Europe (Barros et al., 2014; Figure S5). For these three biogeographical regions, there would be a substantial increase in the annual mean temperature and mean temperature of the driest quarter and a decrease in annual precipitation and precipitation of the warmest quarter (Figure S5). These regions will also have increased heat extremes, heavy precipitation events and/or multiple climatic hazards (Barros et al., 2014). These combined changes in temperature and precipitation might cause excessive temperatures, as well as insufficient or excessive moisture, which could limit fungal growth. Relative

FIGURE 5 Area percentage of macrofungi species richness change among different biogeographical regions in the study area under climate change alone and under combined climate and tree distribution change for SRES A2 (a) and SRES B2 (b) in 2080.



to these regions, Arctic or Alpine biogeographical regions are also projected to have increased temperature; however, the predicted temperature in the future is still lower than in other regions. The increasing temperature might not exceed the optimum temperature for fungal growth and thus would not cause a decrease in macrofungal richness; instead, the warming climate could promote more fungal growth in these regions.

4.3 | Uncertainty

Although this study explored the potential response of macrofungi to future climate and tree distribution change, the observed distribution in the future could be complex, potentially introducing uncertainty to the results.

Dispersal limitation is one of the processes influencing the successful colonization of species (Gao et al., 2015; Jönsson et al., 2008). Unfortunately, the dispersal ecology of most macrofungi remains poorly understood. Some fungi were found to be capable of long-distance dispersal by airborne spores, although a large number of spores fall within a few metres of the fruiting bodies (Möykkönen et al., 1997; Penttilä et al., 1999; Rolstad et al., 2004). However, some fungi can disperse spores over distances of more than 300 km (Edman et al., 2004; Kallio, 1970; Risbeth, 1959). Therefore, some species predicted to have a reduced habitat in our study area might shift to other European regions. Even if fungi can disperse greater distances, the survival of a fungal species will involve an array of biotic interactions with other fungal species and abiotic interactions with other influencing factors (e.g. nitrogen deposition, soil conditions, etc.; Arnolds, 1991; Gange et al., 2011). Moreover, several

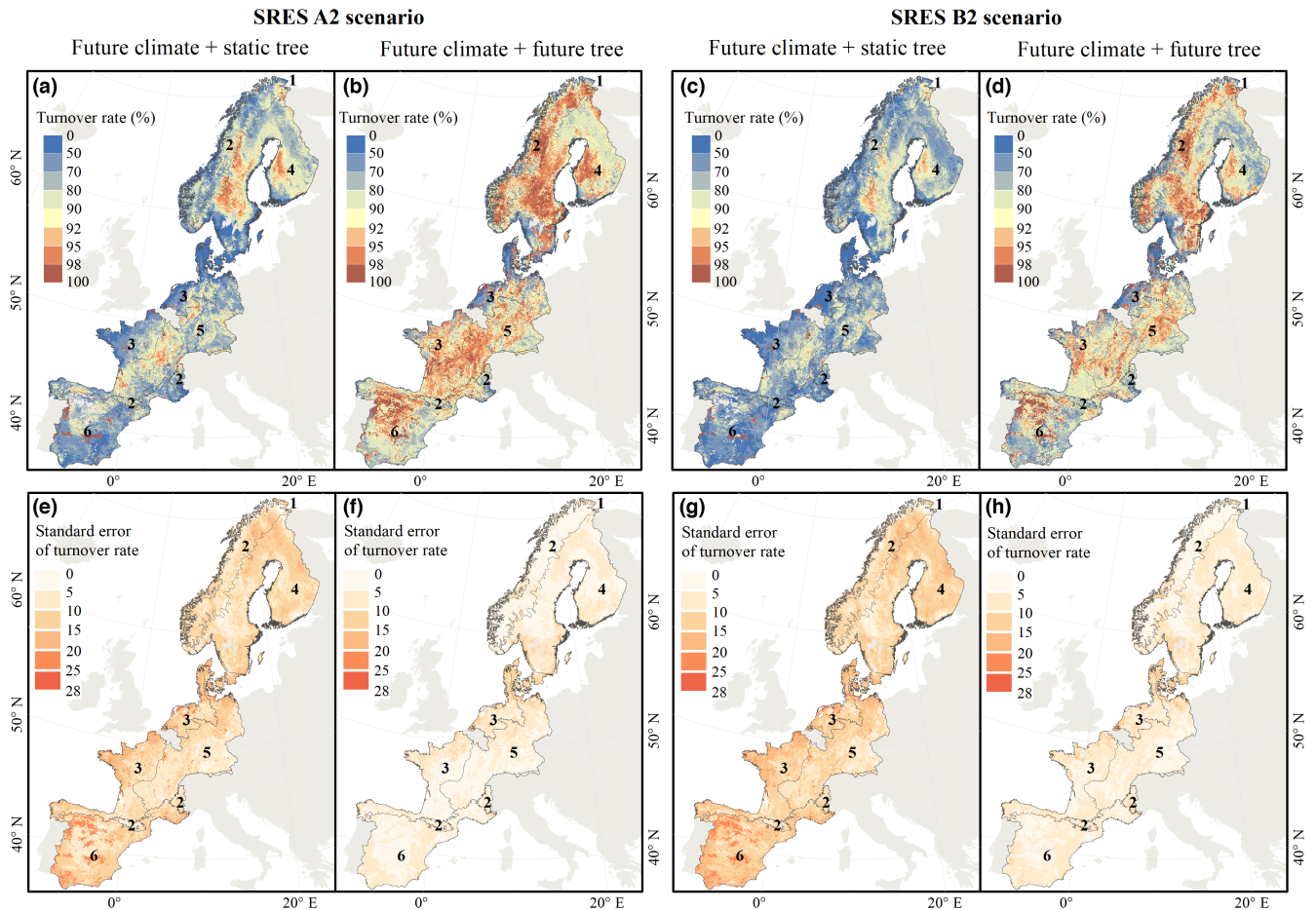


FIGURE 6 Spatial pattern of macrofungi species turnover rate (a–d) and the standard errors of the turnover rate calculated across methods (e–h) under climate change alone (a, c, e and g) and under combined climate and tree distribution change (b, d, f and h) for SRES A2 (a, b and e, f) and SRES B2 (c, d and g, h) in 2080. The number on the study area map shows the biogeographical regions in the study area: 1 Arctic, 2 Alpine, 3 Atlantic, 4 Boreal, 5 Continental and 6 Mediterranean. Turnover = $100 \times (L_s + G_s) / (SR + G_s)$, where SR is the current species richness; L_s is the number of species predicted to disappear from the given pixel; and G_s is the number of species that are currently absent but predicted to migrate in the given pixel.

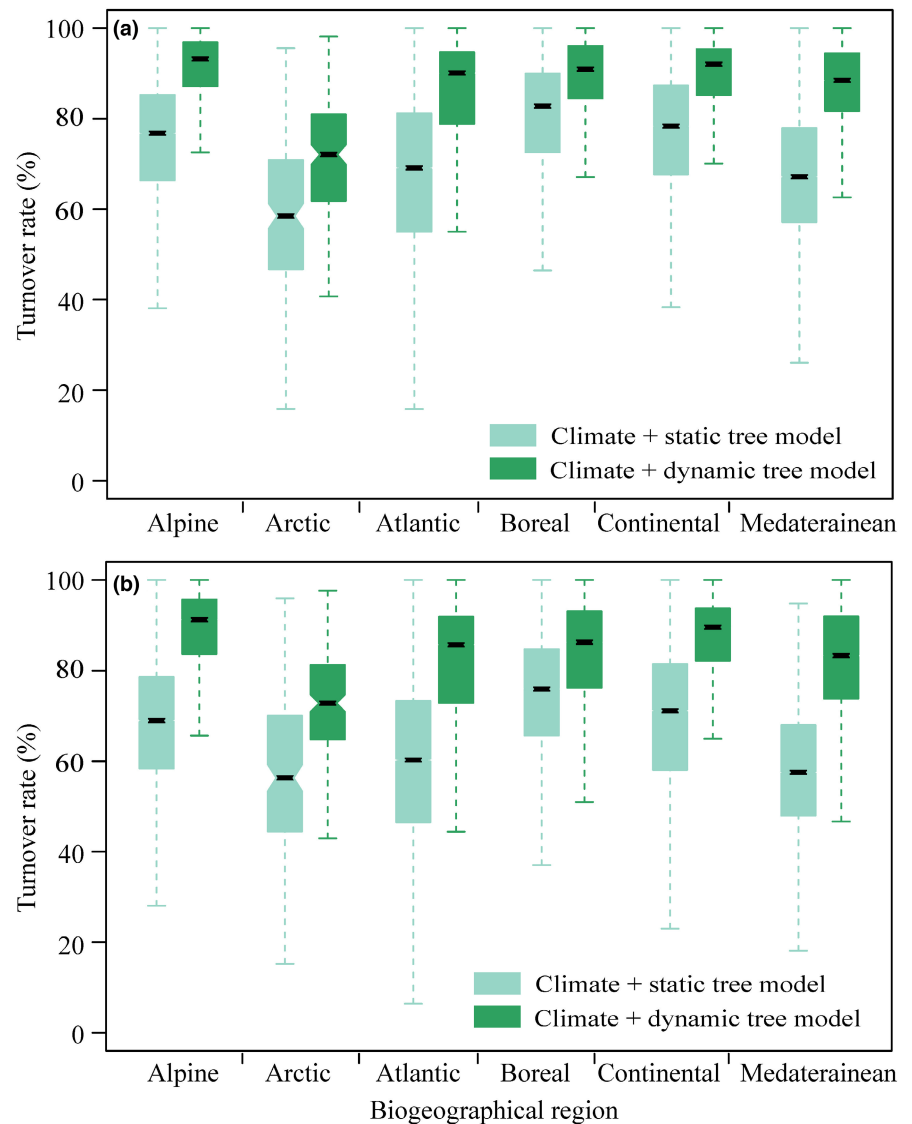
studies have shown that some fungal species have changed hosts and that some tree species have also become hosts for a wider range of fungal species (Botnen, 2020; Gange et al., 2011). Thus, there may be intraspecific trait variability of macrofungi species caused by local adaptation or phenotypic plasticity (Krah & Bässler, 2021), which could assist the survival of macrofungi under environmental change.

In addition, there is also uncertainty introduced by the modelled current and future tree species distribution maps. Mycorrhizal symbiosis, which acquires and transfers water and nutrients from the soil to plants, is an essential interaction between fungi and most vascular plants (Agerer et al., 2012; Bueno et al., 2017; Smith & Read, 2010). Several studies have found that ectomycorrhizal fungi could aid in early tree establishment and growth and promote the survival of tree seedlings (Anthony et al., 2022; Liang et al., 2020). Thus, the redistribution of tree species might also be influenced by their associated fungal species shift. Additionally, ignoring the interaction between fungi and tree species, we should also be aware that climate change impacts species shifting at a different pace, which

could cause a lagging response of tree species to climate change (Lenoir et al., 2020; Vitasse et al., 2021). Thus, the redistribution of tree distribution under future climate change also contains an element of uncertainty.

It should be noted that uncertainties in predicting the potential impacts of climate change may also be introduced by predictor variables and the model itself (Buisson et al., 2010; Heikkinen et al., 2006). To reduce the single model uncertainties and bias, we applied ensemble SDMs in our study. One reason for using ensemble SDMs has been to reduce uncertainty in predictions, especially when compared with a single SDM (Araújo et al., 2005; Grenouillet et al., 2011). Although higher accuracy and significantly more robust predictions have been reported using the averaged ensemble approaches (Araújo & New, 2007; Grenouillet et al., 2011; Marmion et al., 2009), we note that there are geographical inconsistencies in predicting the potential impact of climate change from different models (Figures 4e–h and 6e–h). Areas where predictions are highly inconsistent need greater attention in order to better understand the future impacts of climate change (Buisson et al., 2010). We also

FIGURE 7 Mean turnover rate of macrofungi species in different biogeographical regions under climate change alone (light green) and under combined climate and tree distribution change (green) for SRES A2 (a) and SRES B2 (b) in 2080. The middle line in the box represents the median; the lower box bounds the first quartile; the upper box bounds the 3rd quartile; whiskers represent the upper and lower quartiles. Turnover = $100 \times (L_s + G_s) / (SR + G_s)$, where SR is the current species richness; L_s is the number of species predicted to disappear from the given pixel; G_s is the number of species that are currently absent but predicted to migrate in the given pixel.



note that the distribution of biogeographical regions may change with climate change (Bartsch et al., 2012). In our study, we used static boundaries of biogeographical regions to describe predicted distribution changes in macrofungi species. We have to acknowledge that such static region delineations may not match in the future.

Consequently, the observed response of fungi to future climate and tree species distribution change could be far more complicated. We also have to be careful that the response observed through the aboveground fruiting body could be different from what is observed belowground, though the promotion of fungi fruiting could indicate increased mycelial activity and an improved growth condition of fungi to some degree (Gange et al., 2007). Even though the projected potential response of macrofungi diversity and distribution by the models might not be observed in the future, there could be a close congruence between the two distributions. Despite these uncertainties and limitations, the study provides an indication of the likely effects of climate and tree species distribution change on macrofungi at a large scale,

including the species-specific range change, and species richness, shift and turnover across regions.

5 | CONCLUSIONS

We investigated macrofungi response to future climate and tree species distribution change for a group of relatively conspicuous macrofungi species. To the best of our knowledge, this is the first study modelling the response of a large group of macrofungi species to future climate change at a continental scale across Europe. Our study demonstrates that under future climate change, incorporating tree species distribution change could introduce restrictive effects on macrofungi distributional shifts. Macrofungi response to climate and tree distribution change appears heterogeneous, varying among species and regions. Our findings provide insights into the response of fungi to climate change, thus highlighting the importance of including tree species in the projection of climate change

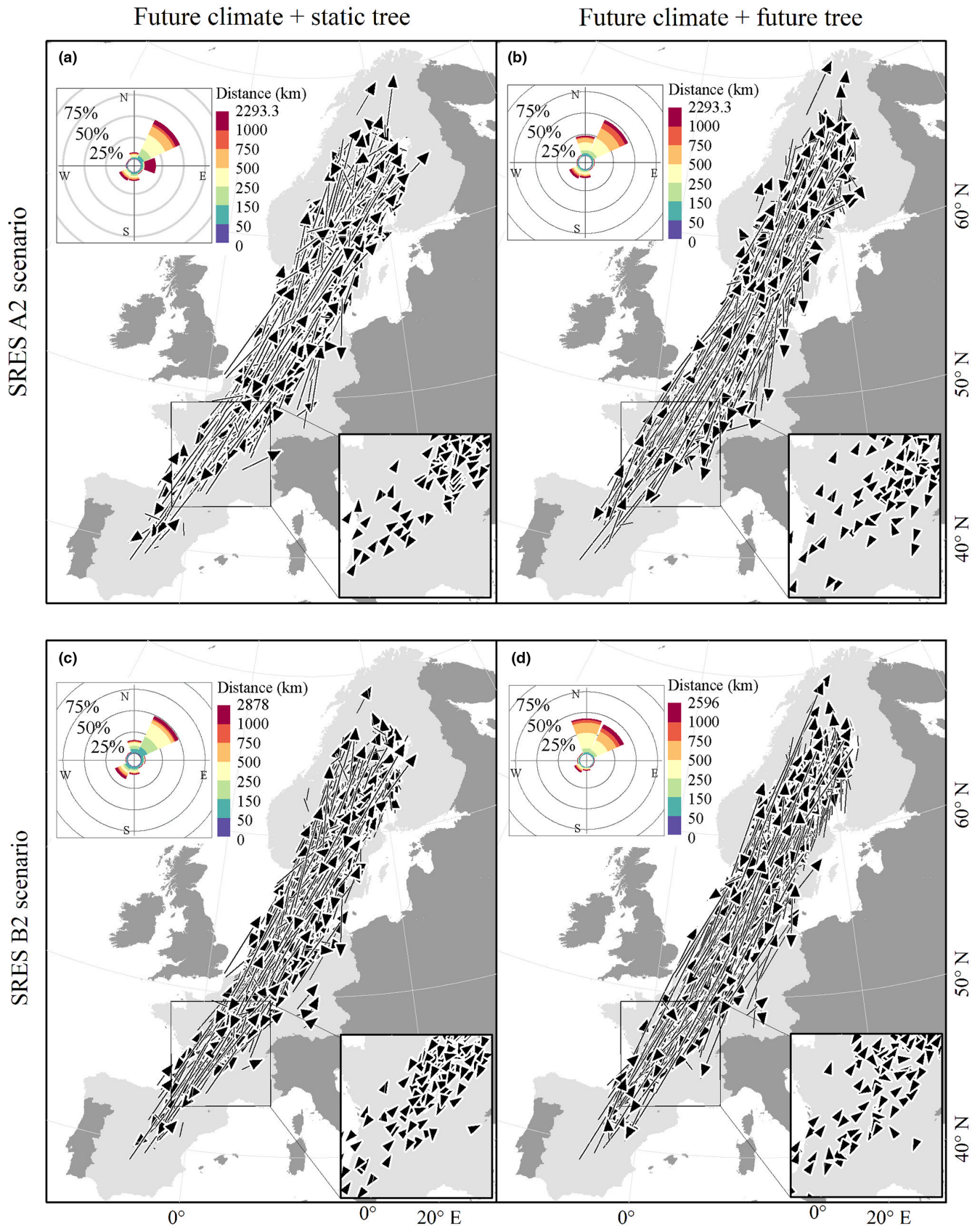


FIGURE 8 Projected spatial shift of macrofungi distribution under climate change alone (a and c) and under combined climate and tree distribution change (b and d) for SRES A2 (a, b) and SRES B2 (c, d). The shift is calculated based on the species range centroid (geometric centre). The arrows represent the direction and magnitude of change at the centroid of each species. The wind roses on the top-left corner of each map summarize the distance and direction of shift for all species; the colours of the bar on each wind rose represent the shift distance (magnitude in km), while the length of each colour bar indicates the proportion of species at that shift distance interval. The map at the bottom right corner showed the shifted direction of species in the zoomed area in France.

impacts on the diversity and distribution of macrofungi on a continental scale.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All datasets used are third-party datasets available freely on public repositories. The occurrence data for fungal species are freely available from the Global Biodiversity Information Facility (www.gbif.org). Climatic data under future scenarios are available from CCAFS-Climate data portal website (http://www.ccafs-climate.org/data_spatial_downscaling/). Tree species distribution maps are available from the European Commission (<https://data.jrc.ec.europa.eu/dataset?pw=1&contributor=Casalegno%20Stefano&q=Suitability%20maps%20of&sort=modified>). The fungal occurrence data used in this study are available at: <https://doi.org/10.15468/dd.ucfskn>; and all other input files and R scripts to reproduce our models are available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.zpc866tbq>.

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BIOSKETCH

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SUPPORTING INFORMATION

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