Agricultural and Forest Meteorology 319 (2022) 108918

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Historical and future spatially-explicit climate change impacts on mycorrhizal and saprotrophic macrofungal productivity in Mediterranean pine forests

Albert Morera[a,b,*], Juan Martínez de Aragón[c], Miquel De Cáceres[d], José Antonio Bonet[a,b], Sergio de-Miguel[a,b]

[a] Department of Crop and Forest Sciences, University of Lleida, Av. Alcalde Rovira Roure 191, E-25198 Lleida, Spain
[b] Joint Research Unit CTFC – AGROTECNIO – CERCA, Ctra. Sant Llorenç de Morunys km 2, 25280 Solsona, Spain
[c] Forest Science and Technology Centre of Catalonia, Ctra. Sant Llorenç de Morunys km 2, 25280 Solsona, Spain
[d] CREAF, E08193 Bellaterra (Cerdanyola del Vallès), Catalonia, Spain

A R T I C L E I N F O

Keywords:
Fungi
Global warming
Random forest
Spatio-temporal dynamics
Saprotrophic
Mycorrhizal

A B S T R A C T

Fungi are responsible for many of the processes that occur in natural ecosystems and largely determine forest ecosystem dynamics, such as the ability of trees to access limiting nutrients and sequester carbon. Understanding and predicting climate change impacts on fungal dynamics over large scales is key in order to gain further insights into the effects of global change on natural ecosystem functioning and related ecosystem services. In this study, we use predictive models based on machine learning algorithms to estimate, in a spatially explicit way, the historical and future (1976–2100) evolution of mycorrhizal and saprotrophic macrofungal productivity in Mediterranean forest areas under climate change scenarios. The greatest changes in total productivity, as well as mycorrhizal fungi, are predicted to occur in subalpine and montane pine forests, where fungal productivity is estimated to decrease, and will be more pronounced under climate change scenarios with higher expected increase in temperature. In contrast to mycorrhizal species, saprotrophic fungi could benefit from pronounced changes in climate and increase their productivity in supra- and mesomediterranean regions at mid-range elevations. Moreover, we estimated that fungal productivity has also changed historically in some scattered areas where changes in climate over the years may have led to a decrease in productivity. This study contributes to raising awareness on the need for anticipating potential global change impacts on this key element of ecosystem functioning, and for deploying possible management policies oriented toward maintaining the important role of fungal productivity in both climate change mitigation and adaptation.

1. Introduction

Climate change is affecting ecological systems at different spatial-temporal levels (Menzel and Fabian, 1999; Kröel-Dulay et al., 2015), including fungi and their dynamics (Kauserud et al., 2008; Diez et al., 2013; B.S. Steidinger et al., 2020). Therefore, understanding and forecasting climate change impacts on fungal productivity is crucial in order to gain further insights into broader impacts on natural ecosystems since fungi are responsible for many of the processes that occur in forest ecosystems. Moreover, fungal productivity also represents a highly valuable non-timber forest resource (i.e. fungal fruitbodies, mushrooms) in many societies and, especially, in the Mediterranean basin (Boa, 2004; Palahí et al., 2009). Given that different fungal species and functional groups are driven differently by climatic, nutritional, or biotic factors, it is expected that different fungal guilds also react differently to changes in the environmental conditions (Kauserud et al., 2008; Diez et al., 2013; Bennett and Classen, 2020; Collado et al., 2019). Thus, mycorrhizal and saprotrophic fungi productivity may be affected differently by climate change and potentially further feed back into climate change impacts.

In Mediterranean ecosystems, where fungal productivity is strongly driven by meteorological and climatic conditions, often within a context of limited water availability (Alday et al., 2017; Karavani et al., 2018; Morera et al., 2021), predicting the potential impacts of climate change

* Corresponding author.
E-mail address: morera.marra@gmail.com (A. Morera).

https://doi.org/10.1016/j.agrformet.2022.108918
Received 29 October 2021; Received in revised form 24 February 2022; Accepted 22 March 2022
Available online 2 April 2022

on fungal productivity is crucial in order to anticipate broad-scale impacts not only on fungal dynamics, but also on the whole forest ecosystem functioning in terms of both climate change mitigation and adaptation. In front of the expected changes in meteorological patterns arising from climate change predictions and their uncertainty, it is also necessary to analyze the potential impacts on fungal productivity by accounting for different scenarios representing alternative representative concentration pathways (RCP) of greenhouse gasses.

A few previous studies have estimated fungal productivity changes either on a small local area or with limited spatial or temporal resolution (Karavani et al., 2018; Ágreda et al., 2015; Morán-Ordóñez et al., 2020; Roces-Díaz et al., 2021), with somewhat opposite findings and conclusions limited by geographical study bias (Bennett and Classen, 2020). In this regard, no previous research has analyzed broader scale impacts of historical and future climate change on fungal productivity across different forest ecosystems and bioclimatic regions. To undertake this challenging task, the availability of unique long-term data series with reliable fungal productivity information is key to better understand and anticipate changes in fungal productivity and related ecosystems services as a result of changes in climatic conditions. Furthermore, the stochasticity that seems to drive fungal fruiting patterns makes evident the need for tools that allow the integration of a large number of predictors and able to reflect the complexity of the relationships, often non-linear, between those variables and fungal productivity. In this regard, machine learning (ML) models are increasingly used for predicting ecologically and socioeconomically important attributes in natural ecosystems (Thessen, 2016; Christin et al., 2019). In particular, it was demonstrated that models based on the random forest algorithm are suitable for estimating mushroom productivity (Morera et al., 2021). These, not being subject to traditional statistical assumptions, can incorporate a large number of variables and find non-linear and complex patterns in the data.

The aim of this study was to estimate and forecast the historical and future evolution (1976–2019 and 2020–2100, respectively) of total, mycorrhizal and soil saprotrophic aboveground macrofungal productivity for different forest ecosystems representing a broad gradient in bioclimatic conditions of the Mediterranean forest biome, namely, subalpine, montane and supra-, meso- and thermomediterranean bioclimatic regions. According to these objectives, we propose three main hypotheses: (1) Due to the strong relationship between fungal ecology and weather-related drivers, the increase in aridity conditions, due to climate change, will negatively affect macrofungal productivity. (2) The different ecological requirements of mycorrhizal and saprotrophic fungi will entail different climate change impacts on the productivity of both functional guilds. (3) Climate change-induced spatio-temporal changes in fungal productivity will be distributed heterogeneously throughout the landscape as a result of fine-grain spatio-temporal variation of historical and future changes in climatic conditions affecting functional guilds differently under alternative climate change. To address these research objectives and hypotheses, we used random forest-based models trained with more than 3000 records of total, mycorrhizal and soil saprotrophic annual fungal productivity and meteorological information of high spatial and temporal resolution to obtain spatially-explicit predictions of historical and future trends in fungal productivity based on historical meteorological records and different climate change scenarios.

2. Materials and methods

2.1. Study area and modeling data

This study has been carried out using data from a permanent network of 131 sampling plots on the western Mediterranean basin sampled weekly during the main fungal fruiting period (between June and December, in the study area) from 1997 until 2019. The 10×10 m plots are randomly distributed along a wide altitudinal and bioclimatic range between 337 and 1992 m above sea level, representing most of the Mediterranean bioclimatic regions and throughout the main pine forest ecosystems of the Mediterranean basin (see Fig. 1 for more details on bioclimatic regions and pine ecosystems). Fungal fruitbodies (i.e. mushrooms) of all macrofungal species were collected for subsequent taxonomic classification and biomass measurements (see Table S1 for more information on numbers of plot and sampled productivity per bioclimatic region). Through aggregation of weekly fungal productivity data over each sampling year, we obtained annual aboveground productivity of fungi by species, plot and year. Fungal species were further classified into two main functional groups, namely soil saprotrophic (including generalist saprotrophs) and mycorrhizal fungi based on expert knowledge and the existing literature (Agerer 2006; Hobbie and Agerer 2010; Tedersoo et al., 2014). More information on the experimental design can be found in Martínez de Aragón et al. (2007).

Meteorological information for each plot was obtained from the weighted mean of interpolated and altitudinally corrected values of different weather variables retrieved from the Meteorological Service of Catalonia (SMC) and the Spanish Meteorological Agency (AEMET) meteorological stations surrounding each sampling plot. Namely, daily precipitation as well as average, maximum, and minimum daily temperature of each plot were obtained using the R package "meteoland" (De Cáceres et al., 2018).

2.2. Modeling

The evolution of fungal productivity over time in a climate change context was predicted on a yearly basis. Meteorological data were aggregated at the monthly level to provide information across the fungal fruiting season and to reduce in a meaningful way the number of potential model predictors compared to working on a daily or weekly scale.

We trained random forest (RF) models to predict total, mycorrhizal and saprotrophic annual fungal productivity using the "ranger" R package (Wright and Ziegler, 2017). In combination with an environmental blocking strategy (Roberts et al., 2017), RF allows for finding ecologically consistent non-linear relationships between a large set of variables in the prediction of fungal productivity under environmental conditions beyond the range of the modeling data, making it suitable for assessing climate change impacts (Morera et al., 2021). Potential predictors to be used in the models were selected based on relative importance within the candidate models (as represented by the mean decrease in node impurity of random forest decision trees), the Spearman correlation between annual fungal productivity and climate variables, and between climate variables (see Table S2 and Figure S1 to S3 for detailed information on the variables used). A proper selection of predictor variables allows for reducing the number of predictors achieving a better interpretation of the models (Coelho et al., 2019), also increasing the similarity between the range of environmental conditions represented in the modeling data and the past and future environmental conditions throughout the study area (Morera et al., 2021).

The hyperparameters “mtry” (number of variables randomly sampled as candidates at each split), “min.node.size” (minimum size of terminal nodes), and “num.trees” (number of trees to grow) of each random forest model were tuned using a Bayesian model-based optimization focused on reducing the prediction error (RMSE) as implemented in the R package "mlr3mbo" (Kotlarski et al., 2014). The hyperparameters abbreviations were based on the terminology used in the R “ranger” package (Wright and Ziegler, 2017). The search space for hyperparameters optimization was defined by the hyperparameters ranges shown in Table S3 using a resampling strategy based on environmental blocking (Roberts et al., 2017).

Models were evaluated based on their predictive accuracy, as well as the ecological interpretation of the variables used to train them. The predictive accuracy of models was assessed from an environmental cross-validation using the average of the root mean square error (RMSE) of 10 folds. Due to the expected differences between past and future

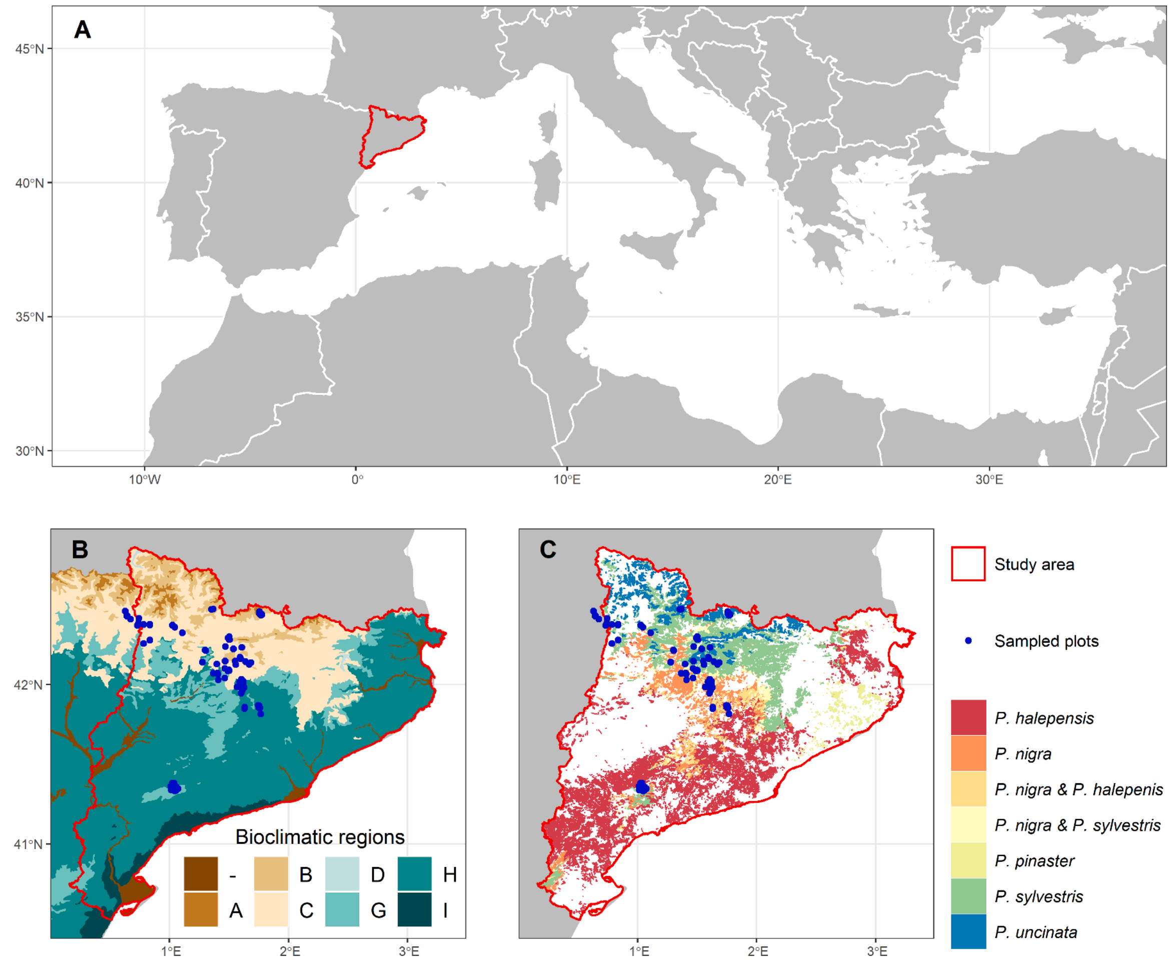

Fig. 1. Study area (red polygon) location in the Mediterranean basin (A), bioclimatic regions of the study area (B), and main pine forest ecosystems of the study area where mushroom productivity was estimated (C). Blue dots (in figures B and C) correspond to the sampled plots. In figure B, different bioclimatic regions are represented by letters as follows: A-alpine, B-subalpine, C-montane, D-foothill, G-supramediterranean, H-mesomediterranean, and I-termomediterranean (according to Rivas-Martínez (1987)). The dark brown areas (“-”) in figure B are not assigned to any bioclimatic region. Coordinates system: WGS 84.

climatic conditions, the use of an environmental blocking aimed at representing appropriately the prediction error of the models in a climatically differentiated environment. Partial dependence plots (PDPs) were used to depict and understand the patterns in the training dataset between fungal productivity and model predictors. The resulting PDPs were evaluated on the basis of existing scientific and expert knowledge in order to assess whether they followed ecologically consistent patterns.

2.3. Assessment of past and future climate change impacts

To assess the historical and future evolution of annual fungal productivity, we used meteorological data for the periods 1976–2019 and 2020–2100 at 1-km resolution, respectively. Historical meteorological information were obtained from the weighted mean of interpolated and altitudinally corrected values of the variables retrieved from SMC and AEMET. Daily future climate projections were obtained from the EURO—CORDEX initiative (Kotlarski et al., 2014). We selected simulations based on two Global Circulation Models (GCM), three Regional Climate Models (RCM) (see couples in Table S4), partly based on the criteria described by Fargeon et al. (2020) in a region adjacent to our study area, and then compared using two contrasted greenhouse gasses emissions, namely, RCP 4.5 and RCP 8.5 (IPCC, 2014). Future RCPs projections of daily precipitation and temperature were downscaled (according to local topography using the reference period 1990–2005) and bias-corrected at 1-km resolution using interpolated historical weather as reference. Interpolations, downscaling and corrections were made with the R package "meteoland" (De Cáceres et al., 2018).

Historical and projected future trends in annual fungal productivity were predicted at the landscape level based on CORINE habitat (Moss and Wyatt, 1994) maps at 1-km resolution (Fig. 1). The forest extent over time was considered constant and with the current pine forest distribution in the study area. Historical fungal productivity was obtained for each 1-km^2 pixel and year for the period 1976–2019. Similarly, future fungal productivity was estimated for the different scenarios defined by the alternative aforesaid RCPs and GCM-RCM couples for the period 2020–2100. To evaluate differences between different RCPs, the average fungal productivity of each GCM-RCM couple was used. Moreover, the average annual fungal productivity over the whole study region was also estimated by computing the mean of all the per pixel values obtained throughout the study area. Once spatially explicit annual predictions of total, mycorrhizal and saprotrophic fungal productivity were obtained for the historical and future periods, for each pixel we assessed the statistical significance of the historical and future trends in fungal productivity using the Mann-Kendall test (Mann, 1945). Moreover, Theil-Sen's approach (Sen, 1968) was used to assess the magnitude of those statistically significant trends (i.e. significant changes in total, ectomycorrhizal or saprotrophic fungal productivity). The Mann-Kendall test and Theil-Sen approach were conducted using the R packages "Kendall" (McLeod, 2011) and "mblm" (Komsta, 2019), respectively. Finally, spatially explicit predictions (i.e., maps) of the historical and future evolution of fungal productivity at the landscape (i.e. regional) level was obtained for the different RCPs. Moreover, the overall trend for the whole study area was obtained by averaging over the productivity values of each pixel throughout the study region. Finally, to relate spatially explicit historical and future changes in fungal productivity to spatially explicit changes in climatic conditions, we also estimated the statistical significance and magnitude of the changes in the meteorological patterns represented by model predictors using the Mann-Kendall test and the Theil-Sen approach.

3. Results

3.1. Predictive accuracy of fungal productivity

RF models explained 42% of the variance of total fungal productivity, and 40% and 20% of mycorrhizal and saprotrophic fungal productivity, respectively. Environmental cross-validation resulted in a prediction error of 133 $kg \cdot ha^{-1} \cdot yr^{-1}$ in terms of RMSE for the models of total fungal productivity. RMSE for mycorrhizal and saprotrophic fungal productivity models was 128 and 19 $kg \cdot ha^{-1} \cdot yr^{-1}$, respectively. The optimal hyperparameters for each model are shown in Table S5.

3.2. Relationships between fungal productivity and meteorological conditions

The adjusted models gave higher relative importance to precipitation variables (~70%) compared to the mean monthly maximum temperature variables (~30%). The models for total and mycorrhizal fungal productivity showed greater importance of precipitation between August and October and the mean maximum temperature between August and October. On the other hand, the model for saprotrophic fungal productivity gave greater importance to October precipitation, followed by rainfall in August, September, and November (Fig. 2 and S4).

PDPs described a positive relationship between annual fungal productivity and monthly rainfall. The models for total and mycorrhizal fungal productivity described continuous nonlinear increase of productivity with increasing precipitation of August and October, whereas the relationship with September and November precipitation was step-shaped. On the other hand, saprotrophic fungal productivity was predicted to increase exponentially only with increasing October precipitation. The mean maximum temperature of August, September and October showed a negative relationship with total and mycorrhizal fungal productivity, while the effect of November precipitation was slightly positive (Fig. 2 and S4).

3.3. Assessment of historical and projected climate change impacts on fungal productivity

Our results showed that the historical change (between 1976 and 2019) in mean total fungal productivity for both the study region as a whole and the different bioclimatic regions was not statistically significant (Table 1 and S6, Fig. 3B and 4). However, the spatially-explicit analysis indeed revealed statistically significant changes in total

Table 1
Historical and projected future changes in average annual fungal productivity ($kg \cdot ha^{-1} \cdot yr^{-1}$) in the study area. Trends are calculated from Theil-Sean approach.

	GCM-RCM	Historical	RCP 4.5	RCP 8.5
Total fungi	Mean	-0.75	0.31	-0.23
	MPI - RCA4	–	*-0.10*	*-0.20*
	MPI - REMO2019	–	*-0.06*	*-0.48**
	CNRM - RCA4	–	*0.42*	*-0.21*
	CNRM – CCLM4–8–17	–	*0.51*	*-0.30**
Mycorrhizal fungi	Mean	-0.49	0.18	-0.23*
	MPI - RCA4	–	*-0.08*	*-0.14*
	MPI - REMO2019	–	*-0.06**	*-0.33**
	CNRM - RCA4	–	*-0.29*	*-0.18**
	CNRM – CCLM4–8–17	–	*-0.42*	*-0.42**
Saprotrophic fungi	Mean	-0.06	0.02	0.03*
	MPI - RCA4	–	*-0.03*	*-0.06*
	MPI - REMO2019	–	*-0.01*	*0.01*
	CNRM - RCA4	–	*-0.02*	*-0.02*
	CNRM – CCLM4–8–17	–	*0.03*	*-0.06*

* Denotes a statistically significant trend according to the Mann-Kendall test.

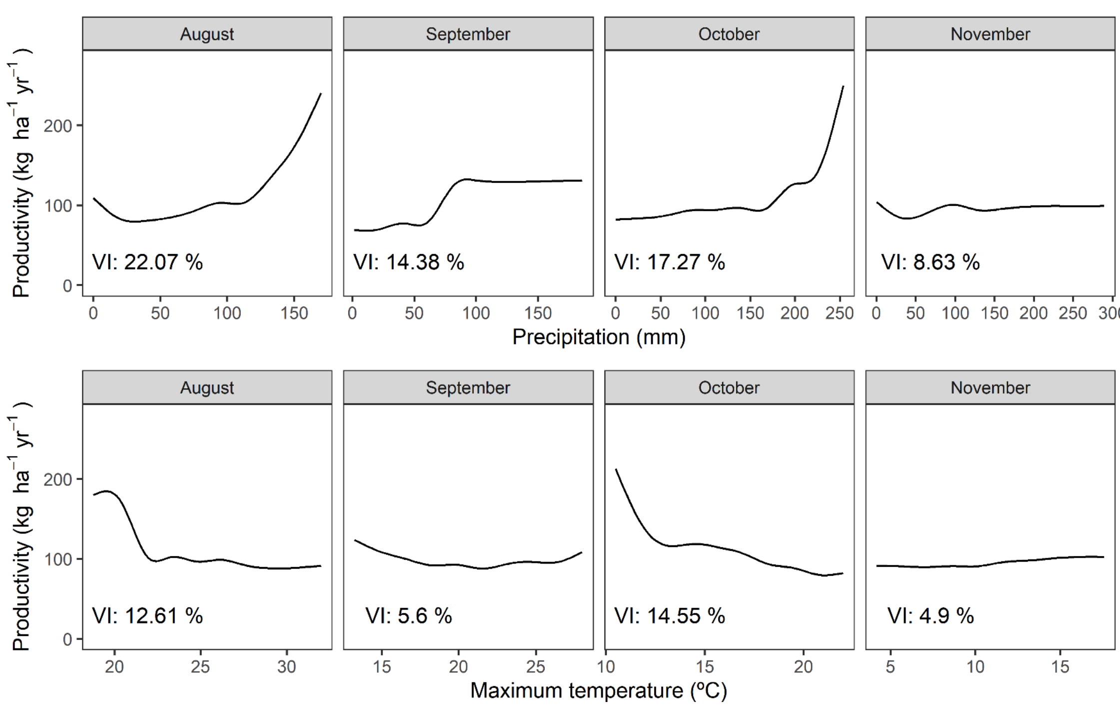

Fig. 2. Partial dependence between model predictors and total fungal productivity across the range of model training meteorological data. VI shows the relative variable importance of each predictor in terms of the mean decrease in node impurity.

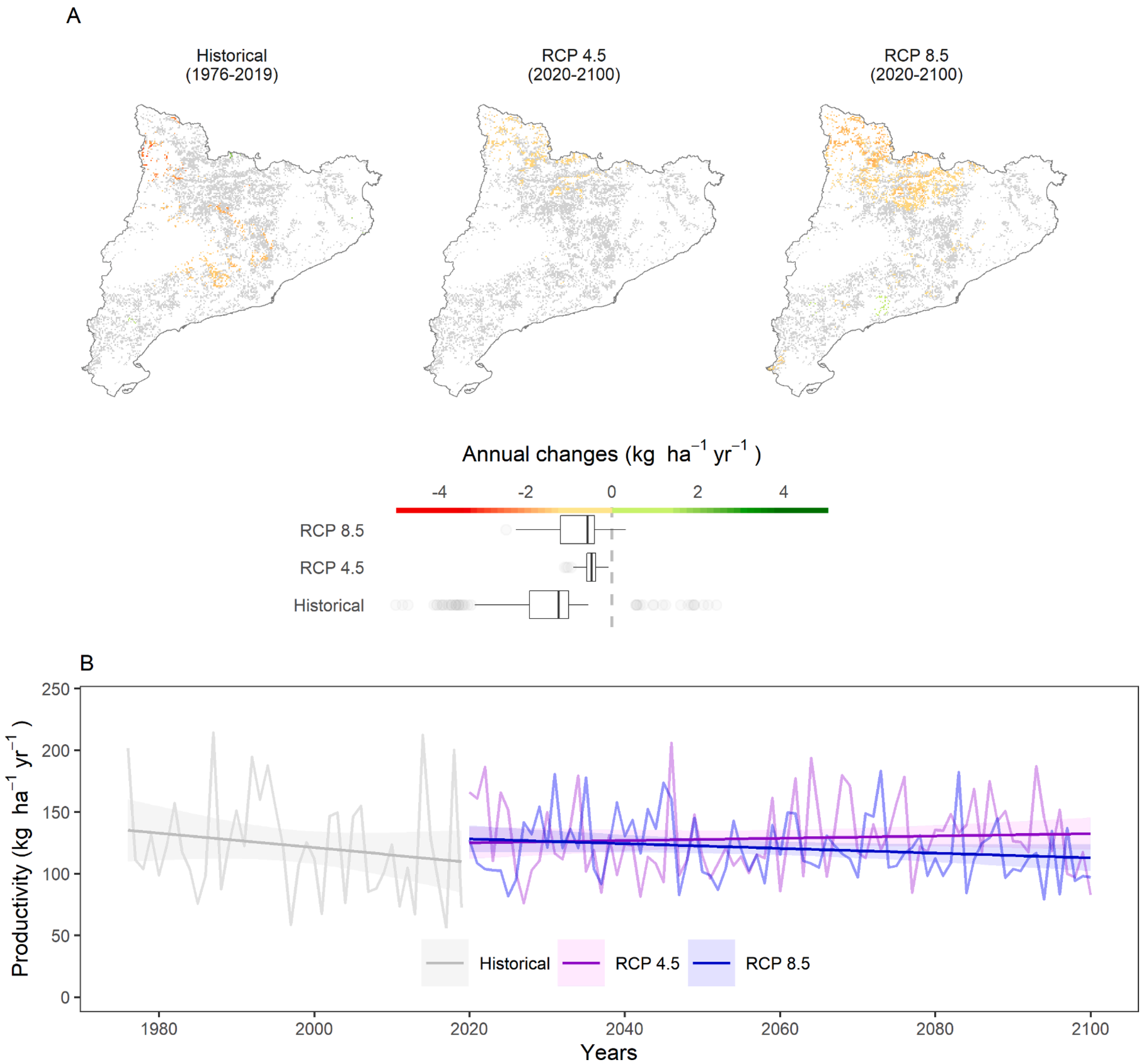

Fig. 3. Historical and future changes in total fungal productivity. Future RCP 4.5 and 8.5 projections were obtained by averaging the spatially explicit fungal productivity over each of GCM-RCM couples. (A) Spatially explicit changes across the study area. gray areas represent no statistically significant changes. Box-plots summarize the range of statistically significant changes in fungal productivity in each map as represented by the legend. (B) Mean fungal productivity trend across bioclimatic regions for the whole study area. Straight lines show the linear trend with a 95% confidence interval (shaded areas).

productivity at some locations throughout the study area, scattered from the subalpine to the mesomediterranean bioclimatic regions and ranging from -5.02 to -0.55 kg·ha^{-1}·yr^{-1} and with a mean reduction of -1.47 kg·ha^{-1}·yr^{-1}. The areas with a statistically significant increase in total fungal productivity were scattered and localized in a few subalpine pure stands of *Pinus uncinata* and *P. sylvestris*, with a fungal productivity increase ranging from 0.55 to 2.42 kg·ha^{-1}·yr^{-1} (Fig. 3A). Mycorrhizal and saprotrophic fungal productivity showed similar trends as described for all fungal species altogether. Namely, there was no statistically significant reduction in mean fungal productivity at the level of the whole study region nor at the bioclimatic region level, but statistically significant (both positive and negative) changes were found within different areas and bioclimatic regions (Table S6, Fig. 3, 4 and S5). While the patterns for mycorrhizal species were almost identical to those of total fungal productivity, saprotrophic fungi were predicted to decrease mostly in subalpine and montane *P. uncinata* and *P. sylvestris* forests. The expected historical reduction in fungal productivity in those areas with predicted statistically significant changes was of -1.21 kg·ha^{-1}·yr^{-1} (ranging from -5.08 to 2.14 kg·ha^{-1}·yr^{-1}) for mycorrhizal fungi, and -0.15 kg·ha^{-1}·yr^{-1} (ranging from -0.26 to 0.17 kg·ha^{-1}·yr^{-1}) for saprotrophic fungi.

Projections of future productivity considering all fungal species differed between RCPs. At the level of the whole study region, mean fungal productivity was not predicted to change significantly during 2020–2100 under RCP 4.5 and RCP 8.5 (Table 1, Fig. 3B). However, for RCP 4.5, the spatially explicit analysis revealed a statistically significant decrease in productivity in subalpine *P. uncinata* and *P. sylvestris* forests (with a mean value of -0.48 kg·ha^{-1}·yr^{-1}, ranging from -1,10 to -0.07 kg·ha^{-1}·yr^{-1}), while total fungal productivity was predicted to remain more stable in the other bioclimatic regions. Furthermore, under RCP 8.5, total fungal productivity was predicted to decrease more generally and to a greater extent in subalpine *P. uncinata* and *P. sylvestris* forests and many of the montane *P. sylvestris* forests (about 2.5-fold higher compared to RCP 4.5, and a mean value of -0.78 kg·ha^{-1}·yr^{-1}, ranging from -2.45 to 0.32 kg·ha^{-1}·yr^{-1}). In contrast, total productivity was not predicted to experience any significant changes in supra- and meso-mediterranean pine forests under any climate change scenario. We only found a predicted decrease in total fungal productivity for some supra-mediterranean forests in the southern part of the study area dominated by *P. nigra* and *P. sylvestris*. Statistically significant increases in total productivity were only predicted for some coastal locations of meso-mediterranean *P. halepensis* forests under the RCP 8.5 scenario, but they

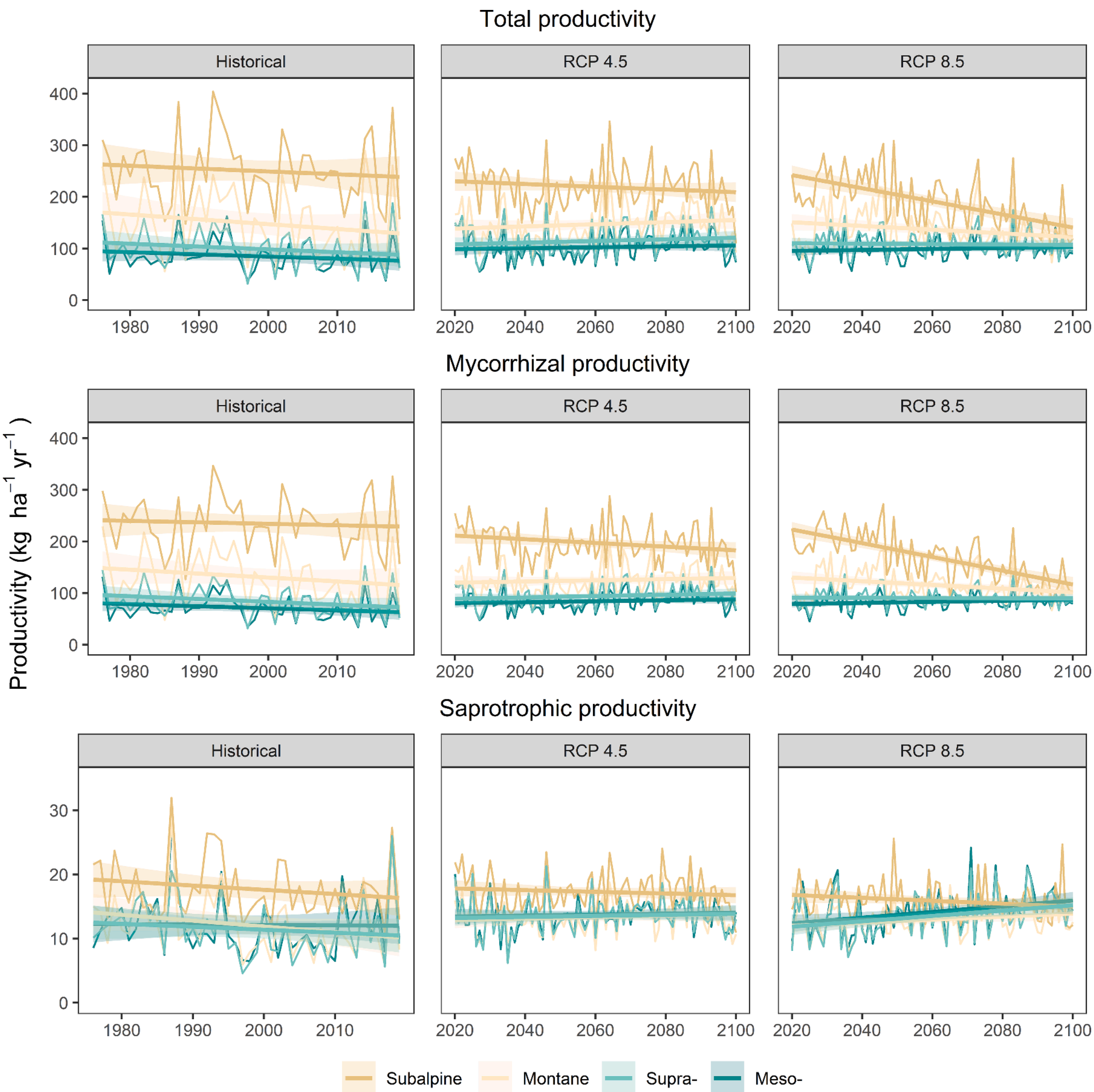

Fig. 4. Predicted historical and future (under RCP 4.5 and RCP 8.5) mean fungal productivity trends in subalpine, montane, supra- and mesomediterranean bioclimatic regions. Straight lines show the linear trend with a 95% confidence interval (shaded areas). Numerical information relating to this table is described in Table S6.

were merely marginal (Fig. 3A). At the bioclimatic region level, this results in a statistically significant decrease in total fungal productivity in the subalpine and montane regions under RCP 8.5, while there was no decrease neither in the supra- and mesomediterranean regions under RCP 8.5 nor in any of the bioclimatic regions under RCP 4.5 (Fig. 4 and Table S6).

Regarding both fungal functional groups, we found that none of them was predicted to experience any statistically significant change in mean fungal productivity for the whole study area under the RCP 4.5 scenario. Conversely, under RCP 8.5 we predicted a significant decrease of -0.23 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$ in mean fungal productivity of mycorrhizal fungi, and a significant increase of 0.03 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$ in the case of saprotrophic fungi (Table 1). The spatially explicit changes under different climate change scenarios for mycorrhizal species were very similar to those predicted for all fungal species altogether. For saprotrophic species, statistically significant changes were found in subalpine *P. uncinata* forests under RCP 4.5, with a mean reduction of -0.03 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$, ranging from -0.08 to 0.05 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$ (but not statistically significant at the whole region level). Under RCP 8.5, we found that the area where productivity was predicted to decrease was similar to RCP 4.5, while the area where production is predicted to increase in the future, namely, supra- and mesomediterranean, became larger, showing an overall increase of 0.03 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$ (ranging from -0.10 to 0.08 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$) in supra- and mesomediterranean pine forests dominated by pure stands of *P. halepensis* and *P. nigra* and mixed stands of *P. nigra* with *P. halepensis* or *P. sylvestris* (Fig. 4, 5 and Table S6).

Regarding the spatially explicit level of analysis, a reduction in the predicted total and mycorrhizal fungal productivity was found in different bioclimatic regions for both historical and future periods. While in the future climate change scenarios the changes in productivity were concentrated in subalpine and montane pure stands of *P. uncinata* and *P. sylvestris* of the Pyrenean mountain range (northern part of the study area), during the historical period analyzed, the predicted changes were rather distributed in small clusters scattered throughout the territory. Regarding saprotrophic fungi, the differences between the historical and future periods were more remarkable. Both in the historical period and RCP 4.5 a decrease in fungal productivity was estimated in subalpine forests of *P. sylvestris* and *P. uncinata*, whereas in the RCP 8.5 scenario the trend was an increasing one in the rest of bioclimatic regions (Fig. 5).

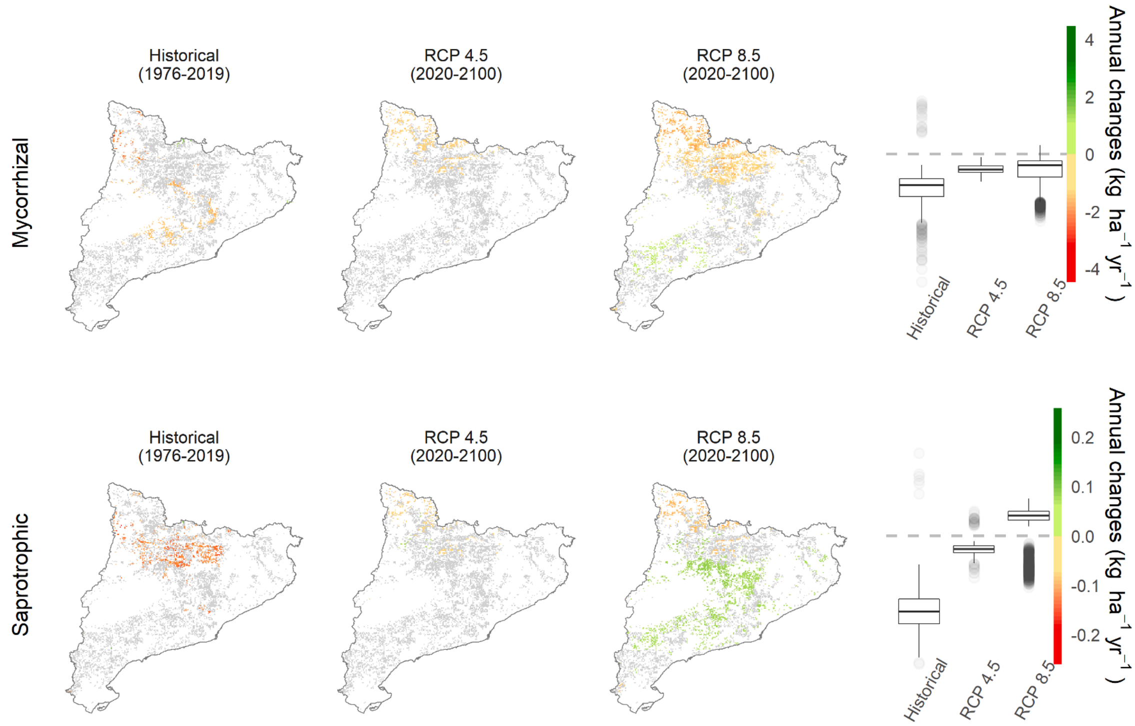

Fig. 5. Spatially explicit historical and future changes in mycorrhizal and saprotrophic fungal productivity. Box-plots summarize the range of statistically significant changes in fungal productivity in each map as represented by the legend. Future RCP 4.5 and 8.5 projections were obtained by averaging the spatially explicit fungal productivity over each of GCM-RCM couples. gray areas represent no statistically significant changes.

It is worth noting the differences in fungal productivity estimates derived from different GCM-RCM couples. In the RCP 4.5, total fungal productivity in Mediterranean forests of the study area were predicted to drop more under the MPI-M-MPI-ESM-LR model compared to the CNRM-CERFACS-CNRM-CM5. Conversely, these differences are not evident in RCP 8.5 (Table 1 and Figures S6 and S7).

4. Discussion

This is the first study that we are aware of to assess spatially explicit historical and future changes in fungal productivity in natural ecosystems, using predictive models. Until now, climate change-induced shifts in fungal productivity have only been studied at a very local scale and without taking into account a broad bioclimatic gradient over a large study region (Karavani et al., 2018; Ágreda et al., 2015; Morán-Ordóñez et al., 2020). Our study was performed using the largest spatial-temporal fungal productivity monitoring dataset from Mediterranean forests, resulting from a consistent sampling and taxonomic identification within more than a hundred permanent sampling plots monitored for more than twenty years, which overcomes most of the problems suggested by Hao et al. (2020) regarding the modeling of fungal resources. These data allowed us to work with a high spatial resolution, which is crucial when predicting fungal biogeographic patterns, since small changes in environmental conditions may imply large changes in fungal productivity (Morera et al., 2021).

This study shows that fungal productivity in Mediterranean forests has been and will be affected by climate change in different ways across large-scale landscapes (with different bioclimatic regions) and under different climate change scenarios. Changes in fungal productivity in RCP 4.5 were almost non-existent, showing that in a context where greenhouse gasses emissions were reduced over the next decades (IPCC, 2014), it may be possible to minimize the impact of climate change on fungal productivity and related ecological processes. Nevertheless, in the more severe climate change scenario (RCP 8.5), changes in fungal productivity are predicted to be much more widespread. Similar differences between RCPs were reported to affect fungal species richness and abundance in North American boreal forests (B.S. Steidinger et al., 2020) and the distribution of specific species in China (Guo et al., 2017). However, there is a strong controversy about how fungal productivity will change in front of climate change (Morán-Ordóñez et al., 2021). Boddy et al. (2014), Ágreda et al. (2015) and Thomas and Büntgen (2019) point out that there could be a decrease in mushroom productivity due to a delay in phenology (Büntgen et al., 2015; Kauserud et al., 2012), while Karavani et al. (2018) suggested that mushroom productivity could even increase in certain areas due to a widening of the fruiting season.

These estimated changes in fungal productivity are closely related to observed and forecasted changes in Mediterranean climate (see “Extended Technical Description of Results” in Supplementary Text for details). For both historical and future periods, an overall significant increase in temperature is expected to occur throughout the study region. However, no significant changes are expected to occur in autumn precipitation, except in a few scattered areas (Figures S1 to S3). In addition, those areas with a greater predicted decrease in fungal productivity (*P. sylvestris* and *P. nigra* forests of subalpine and montane regions) were those areas with a greater increase in temperature, especially under RCP 8.5. This suggests that increased temperature as a result of global warming may be the main driver of fungal productivity changes in Mediterranean ecosystems in the long run, even though it is indeed expected that changes in fungal productivity are a consequence of changes in both temperature and precipitation. This is supported from the point of view of species phenology across space due to climate variability (Andrew et al., 2018). Such changes in temperature and fungal productivity became less marked with decreasing altitude within these bioclimatic regions. However, some areas in bioclimatic regions other than the subalpine and montane forests (i. e. *P. sylvestris* and *P. nigra* forests in the southern supramediterranean region of the study area) were predicted to experience a decrease in fungal productivity, but not a greater increase in temperature compared to surrounding areas. In contrast, these areas are predicted to experience a significant decrease in

October precipitation, which is consistent with the delayed fruiting phenology compared to subalpine and montane forests (Karavani et al., 2018).

The spatially explicit analysis of historical trends showed different patterns compared to future projections. This is consistent with the differences between historical and future climate trends observed in the study area (Figures S1 to S3). These different patterns could be partly due to a statistical artifact of using two time periods (historical vs. future) of different length (43 years from 1976 to 2019, compared to 80 years from 2020 to 2100 used in future projections), where the very large inter-annual variability in fungal productivity may partly blur the influence of longer term trends of climate variables. This is also probably the reason of the small break between the historical and future (linear) trend lines of overall fungal productivity (Figs. 3B and S2), even though both lines match within the 95% confidence interval.

We estimate that under both RCP 4.5 and 8.5, the largest and most significant changes in productivity are predicted to occur in *P. sylvestris* and *P. uncinata* forests of subalpine and montane regions. These areas currently host the highest fungal productivity in the study region (de-Miguel et al., 2014; Morera et al., 2021). In these areas, where macrofungi live closer to their physiological limit, it was expected that changes would be greater (J. Diez et al., 2020). In our study area, the greatest change in the higher altitude areas is shown in the shape of a similarly negative exponential relationship between fungal productivity and the average maximum temperature of August and October (both the most important temperature-related variables in our models). This relationship leads to a more pronounced decline in productivity in colder areas for the same increase in temperature.

When dealing with complex orography (such as in many areas throughout the distributional range of Mediterranean forests), the use of statistical downscaling to a resolution of 1 km allowed to improve the spatially explicit estimates. The differences found between future fungal productivity trends described by different GCM-RCM couples highlight the need for evaluating a set of alternative models to minimize the potential prediction bias that may arise from relying on one single model (Knutti et al., 2010). Besides, using RCMs takes on greater importance when making predictions at larger scale at the regional level where, by aggregation, small-scale differences become even more important. Thus, RCMs allow for reducing prediction bias without increasing the uncertainty of GCMs predictions because the biases of both models are neither additive nor independent, resulting in more accurate average estimates of annual fungal productivity (Knutti et al., 2010). This becomes particularly important in areas where a complex orography contributes to notable differences in meteorological and bioclimatic conditions at the regional scale.

In line with the findings reported by Salerni et al. (2002), Kauserud et al. (2008), Büntgen et al. (2013) and Ágreda et al. (2015), we found that the relationships between environmental variables and fungal productivity, as well as the importance given to each predictor in the models, varied depending on the fungal trophic strategy. Such variation reflects differences in the fruiting phenology of the species in each functional group and their ecological requirements (Diez et al., 2013; J. 2020). Since mycorrhizal species start fruiting earlier in our study area, fungal productivity models gave greater importance to predictors referring to August or September weather conditions. On the other hand, since saprotrophic species tend to emerge later, fungal productivity models gave greater importance to predictors related to weather conditions in October. Saprotrophic species are generally found in the soil organic layers (Lindahl et al., 2007; Kluting et al., 2019), making them more sensitive to sudden changes in moisture. This may explain why the models for saprotrophic species productivity gave considerably greater importance to October precipitation (the month of highest saprotrophic fungal productivity) compared to October maximum temperature, whereas in the models for mycorrhizal fungal productivity the differences in variable importance between October precipitation and maximum temperature were much lower. Such differences in variable importance for different fungal functional groups led to distinct predicted productivity trends between mycorrhizal and saprotrophic fungi. Moreover, these changes in mycorrhizal fungal productivity could also be further modulated by the indirect impact of climate change on tree phenology and growth (Egli et al., 2010). It should be noted that both the estimates of mycorrhizal fungal productivity and the relationships with their main drivers are very similar to those found for total fungi. This is because most of the total mushroom biomass in Mediterranean ecosystems (here represented by our dataset) corresponds to mycorrhizal species (Table S1; Ágreda et al., 2015).

The assessed fungal productivity changes along time in a climate change context must be framed within a global shift in Mediterranean natural ecosystems (Guiot and Cramer, 2016). These changes do not only affect fungal productivity per se. Indeed, due to the important role fungi play in natural ecosystems, changes in their biogeographical productivity patterns have the potential to affect the diversity and functioning of forest ecosystems (Gouveia et al., 2017; Santonja et al., 2017). Climate change is predicted to affect the diversity and distribution of mycorrhizal symbioses (Steidinger et al., 2019; B.S. 2020), which determine the ability of trees to access limiting soil nutrients (Batterman et al., 2013; Shah et al., 2016) or to sequester carbon (Clemmensen et al., 2015; Averill et al., 2018). Therefore, changes in the distribution of these symbioses directly affect forest ecosystems' ability to resist the effects of climate change (Terrer et al., 2016). Such changes in forest ecosystems may, in turn, further impact fungal communities, creating a feedback loop leading to accelerated changes in these ecosystems. In addition, since mushrooms are the fruitbodies of fungi where spores are produced, changes in fungal productivity directly affect the spore dispersal of these organisms. Decreased spore production can directly affect the rate of spore arrival and thereby limiting fungal dispersal (Norros et al., 2012). Such spore dispersal limitation plays a key role in shaping the spatial patterns of fungi (Nordén, 2000) and highlights the need to further study the relationship between both.

Due to the lack of consistent projections of other potential drivers of fungal productivity at the landscape level throughout the study area, in this study fungal productivity changes were assessed as a function of changes in climatic conditions, without considering other drivers such as tree species migration or forest structural changes from either environmental or anthropogenic origin. Having this type of information would allow for more accurate prediction of fungal productivity changes and increase the understanding of past, and future forest ecosystem dynamics. However, although changes in structural characteristics of Mediterranean forest stands can have considerable impacts on the provision of different ecosystem services, fungal productivity is likely to be more influenced by climate change due to the direct link between weather conditions and mushroom emergence, especially in water-limited forest ecosystems (Morán-Ordóñez et al., 2020).

5. Conclusions

Our results suggest that climate change is negatively affecting fungal productivity, with subalpine and montane ecosystems (located at higher altitudes) being the most affected. Furthermore, these impacts can differ between fungal trophic strategies. Mycorrhizal fungi productivity (more abundant in terms of total biomass) will decrease in subalpine and montane regions, and more markedly and extensively under RCP 8.5 compared to RCP 4.5. Conversely, saprotrophic fungi productivity could be enhanced in the supra- and mesomediterranean regions under RCP 8.5. This results in a complex mosaic of climate change impacts on fungal productivity across the landscape depending on the relationships found between meteorological drivers and fungal species. In a nutshell, this study sheds light on the need for anticipating potential global change impacts on fungal dynamics, a key element of forest ecosystem functioning, and for deploying management policies oriented toward maintaining the important role of fungal productivity in the provision of multiple ecosystem services, including both climate change mitigation and adaptation.

Declaration of Competing Interest

Authors declare no conflict of interest.

Acknowledgements

We thank the "Agencia Estatal de Meteorología (AEMET)" and "Servei Meteorològic de Catalunya (SMC)" for providing daily weather station data. This work was supported by the Secretariat for Universities and of the Ministry of Business and Knowledge of the Government of Catalonia and the European Social Fund. This work was partially supported by the Spanish Ministry of Science, Innovation and Universities (Grant No. RTI2018–099315-A-I00) and by the National Parks Autonomous Agency (*Organismo Autónomo de Parques Nacionales*, OAPN) (Grant No. 2711/2021). J.A.B. and Sd-M benefitted from a Serra-Húnter Fellowship provided by the Government of Catalonia.

Contributions

JMdA, JAB and Sd-M contributed in the installation of the sampling plots and data collection. AM, MdC and Sd-M analysed the data. AM wrote the manuscript. All authors participated in the review and editing of the manuscript. Sd-M supervised the work during the whole process. The authors read and approved the final manuscript.

Data availability statement

The data that support the findings of this study are available on request from the corresponding authors. The data are not publicly available due to legal and privacy constraints as they are owned by different institutions and affect private forest ownerships.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.108918.

References

Agerer, R., 2006. Fungal relationships and structural identity of their ectomycorrhizae. Mycol. Prog. 5 (2), 67–107. https://doi.org/10.1007/s11557-006-0505-x.

Ágreda, T., et al., 2015. Increased evapotranspiration demand in a Mediterranean climate might cause a decline in fungal yields under global warming. Glob. Chang. Biol. 21 (9), 3499–3510. https://doi.org/10.1111/gcb.12960.

Alday, J.G., et al., 2017. Mushroom biomass and diversity are driven by different spatio-temporal scales along Mediterranean elevation gradients. Sci. Rep. 7 (1), 45824. https://doi.org/10.1038/srep45824.

Andrew, C., et al., 2018. Explaining European fungal fruiting phenology with climate variability. Ecology 99 (6), 1306–1315. https://doi.org/10.1002/ecy.2237.

Averill, C., Dietze, M.C., Bhatnagar, J.M., 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. Glob. Chang. Biol. 24 (10), 4544–4553. https://doi.org/10.1111/gcb.14368.

Batterman, S.A., et al., 2013. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature 502 (7470), 224–227. https://doi.org/10.1038/nature12525.

Bennett, A.E., Classen, A.T., 2020. Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias,. Ecology 101 (4). https://doi.org/10.1002/ecy.2978.

Boa, E., 2004. Wild Edible Fungi a Global Overview of Their Use and Importance to People. Food and Agriculture Organization of the United Nations, Rome, Italy.

Boddy, L., et al., 2014. Climate variation effects on fungal fruiting. Fungal Ecol. 10, 20–33. https://doi.org/10.1016/j.funeco.2013.10.006.

Büntgen, U., et al., 2013. Unraveling environmental drivers of a recent increase in Swiss fungi fruiting. Glob. Chang. Biol. 19 (9), 2785–2794. https://doi.org/10.1111/gcb.12263.

Büntgen, U., et al., 2015. Drought-induced changes in the phenology, productivity and diversity of Spanish fungi. Fungal Ecol. 16, 6–18. https://doi.org/10.1016/j.funeco.2015.03.008.

De Cáceres, M., et al., 2018. Estimating daily meteorological data and downscaling climate models over landscapes. Environ. Model. Softw. 108, 186–196. https://doi.org/10.1016/j.envsoft.2018.08.003.

Christin, S., Hervet, É., Lecomte, N., 2019. Applications for deep learning in ecology. Methods Ecol. Evol. 10 (10), 1632–1644. https://doi.org/10.1111/2041-210X.13256. Edited by H. Ye.

Clemmensen, K.E., et al., 2015. Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. New Phytol. 205 (4), 1525–1536. https://doi.org/10.1111/nph.13208.

Coelho, M.T.P., Diniz-Filho, J.A., Rangel, T.F., 2019. A parsimonious view of the parsimony principle in ecology and evolution. Ecography 42 (5), 968–976. https://doi.org/10.1111/ecog.04228.

Collado, E., et al., 2019. Mushroom productivity trends in relation to tree growth and climate across different European forest biomes. Sci. Total Environ. 689, 602–615. https://doi.org/10.1016/j.scitotenv.2019.06.471.

de-Miguel, S., et al., 2014. Impact of forest management intensity on landscape-level mushroom productivity: a regional model-based scenario analysis. For. Ecol. Manage. 330, 218–227. https://doi.org/10.1016/j.foreco.2014.07.014.

Diez, J., et al., 2020. Altitudinal upwards shifts in fungal fruiting in the Alps. Proc. R. Soc. B: Biol. Sci. 287 (1919), 20192348 https://doi.org/10.1098/rspb.2019.2348.

Diez, J.M., et al., 2013. Predicting species-specific responses of fungi to climatic variation using historical records. Glob. Chang. Biol. 19 (10), 3145–3154. https://doi.org/10.1111/gcb.12278.

Egli, S., et al., 2010. Is forest mushroom productivity driven by tree growth? Results from a thinning experiment. Ann. For. Sci. 67 (5) https://doi.org/10.1051/forest/2010011, 509–509.

Fargeon, H., et al., 2020. Projections of fire danger under climate change over France: where do the greatest uncertainties lie? Clim. Change 160 (3), 479–493. https://doi.org/10.1007/s10584-019-02629-w.

Gouveia, C.M., et al., 2017. Drought impacts on vegetation activity in the Mediterranean region: an assessment using remote sensing data and multi-scale drought indicators. Glob Planet Change 151, 15–27. https://doi.org/10.1016/j.gloplacha.2016.06.011.

Guiot, J., Cramer, W., 2016. Climate change: the 2015 Paris Agreement thresholds and Mediterranean basin ecosystems. Science 354 (6311), 465–468. https://doi.org/10.1126/science.aah5015.

Guo, Y., et al., 2017. Prediction of the potential geographic distribution of the ectomycorrhizal mushroom Tricholoma matsutake under multiple climate change scenarios. Sci. Rep. 7 (1), 46221. https://doi.org/10.1038/srep46221.

Hao, T., et al., 2020. Using Species Distribution Models For Fungi. Fungal Biol. Rev. 34 (2), 74–88. https://doi.org/10.1016/j.fbr.2020.01.002.

Hobbie, E.A., Agerer, R., 2010. Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. Plant Soil 327 (1–2), 71–83. https://doi.org/10.1007/s11104-009-0032-z.

IPCC (2014) *AR5 Synthesis Report: Climate Change 2014*. Geneva, Switzerland.

Karavani, A., et al., 2018. Effect of climatic and soil moisture conditions on mushroom productivity and related ecosystem services in Mediterranean pine stands facing climate change. Agric. For. Meteorol. 248, 432–440. https://doi.org/10.1016/j.agrformet.2017.10.024.

Kauserud, H., et al., 2008. Mushroom fruiting and climate change. Proc. Natl. Acad. Sci. 105 (10), 3811–3814. https://doi.org/10.1073/pnas.0709037105.

Kauserud, H., et al., 2012. Warming-induced shift in European mushroom fruiting phenology. Proc. Natl. Acad. Sci. 109 (36), 14488–14493. https://doi.org/10.1073/pnas.1200789109.

Kluting, K., et al., 2019. Distribution patterns of fungal taxa and inferred functional traits reflect the non-uniform vertical stratification of soil microhabitats in a coastal pine forest. FEMS Microbiol. Ecol. 95 (11) https://doi.org/10.1093/femsec/fiz149.

Knutti, R., et al., 2010. Challenges in Combining Projections from Multiple Climate Models. J. Clim. 23 (10), 2739–2758. https://doi.org/10.1175/2009JCLI3361.1.

Komsta, L. (2019) *mblm: Median-Based Linear Models. R package Version 0.12.1.*Available at: https://cran.r-project.org/package=mblm.

Kotlarski, S., et al., 2014. Regional climate modeling on European scales: a joint standard evaluation of the EURO-CORDEX RCM ensemble. Geoscientific Model Dev. 7 (4), 1297–1333. https://doi.org/10.5194/gmd-7-1297-2014.

Kröel-Dulay, G., et al., 2015. Increased sensitivity to climate change in disturbed ecosystems. Nat. Commun. 6 (1), 6682. https://doi.org/10.1038/ncomms7682.

Lindahl, B.D., et al., 2007. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytol. 173 (3), 611–620. https://doi.org/10.1111/j.1469-8137.2006.01936.x.

Mann, H.B., 1945. Nonparametric Tests Against Trend. Econometrica 13 (3), 245. https://doi.org/10.2307/1907187.

Martínez de Aragón, J., et al., 2007. Productivity of ectomycorrhizal and selected edible saprotrophic fungi in pine forests of the pre-Pyrenees mountains, Spain: predictive equations for forest management of mycological resources. For. Ecol. Manage. 252 (1–3), 239–256. https://doi.org/10.1016/j.foreco.2007.06.040.

McLeod, A.I., 2011. Kendall: Kendall rank Correlation and Mann-Kendall trend test. R package Version 2.2. Available at. https://cran.r-project.org/package=Kendall.

Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature 397 (6721). https://doi.org/10.1038/17709, 659–659.

Morán-Ordóñez, A., et al., 2020. Future trade-offs and synergies among ecosystem services in Mediterranean forests under global change scenarios. Ecosyst. Serv. 45, 101174 https://doi.org/10.1016/j.ecoser.2020.101174.

Morán-Ordóñez, A., et al., 2021. Ecosystem services provision by Mediterranean forests will be compromised above 2°C warming. Glob Chang Biol 27 (18), 4210–4222. https://doi.org/10.1111/gcb.15745.

Morera, A., et al., 2021. Performance of statistical and machine learning-based methods for predicting biogeographical patterns of fungal productivity in forest ecosystems. Forest Ecosyst. 8 (1), 21. https://doi.org/10.1186/s40663-021-00297-w.

Moss, D., Wyatt, B.K., 1994. The CORINE biotopes project: a database for conservation of nature and wildlife in the European community. Appl. Geogr. 14 (4), 327–349. https://doi.org/10.1016/0143-6228(94)90026-4.

Nordén, B., 2000. Dispersal Ecology and Conservation of Wood-Decay Fungi. Göteborg University, Sweden.

Norros, V., et al., 2012. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. Oikos 121 (6), 961–974. https://doi.org/10.1111/j.1600-0706.2012.20052.x.

Palahí, M., et al., 2009. Effect of the inclusion of mushroom values on the optimal management of even-aged pine stands of Catalonia. Forest Sci. 55 (6), 503–511. https://doi.org/10.1093/forestscience/55.6.503.

Rivas-Martínez, S. (1987) *Memoria Del Mapa De Series de Vegetación de España*. Edited by I. C. O. N. A. S. Técnica. Madrid, Spain: Ministerio Agricultura, Pesca y Alimentación.

Roberts, D.R., et al., 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40 (8), 913–929. https://doi.org/10.1111/ecog.02881.

Roces-Díaz, J.V., et al., 2021. Temporal changes in Mediterranean forest ecosystem services are driven by stand development, rather than by climate-related disturbances. For. Ecol. Manage. 480, 118623 https://doi.org/10.1016/j.foreco.2020.118623.

Salerni, E., et al., 2002. Effects of temperature and rainfall on fruiting of macrofungi in oak forests of the Mediterranean area. Isr. J. Plant Sci. 50 (3), 189–198. https://doi.org/10.1560/GV8J-VPKL-UV98-WVU1.

Santonja, M., et al., 2017. Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean oak forest. J. Ecol. 105 (3), 801–815. https://doi.org/10.1111/1365-2745.12711. Edited by R. McCulley.

Sen, P.K., 1968. Estimates of the Regression Coefficient Based on Kendall's Tau. J. Am. Stat. Assoc. 63 (324), 1379–1389. https://doi.org/10.1080/01621459.1968.10480934.

Shah, F., et al., 2016. Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. New Phytol. 209 (4), 1705–1719. https://doi.org/10.1111/nph.13722.

Steidinger, B.S., et al., 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. Nature 569 (7756), 404–408. https://doi.org/10.1038/s41586-019-1128-0.

Steidinger, B.S., et al., 2020. Ectomycorrhizal fungal diversity predicted to substantially decline due to climate changes in North American Pinaceae forests. J. Biogeogr. 47 (3), 772–782. https://doi.org/10.1111/jbi.13802.

Tedersoo, L., et al., 2014. Global diversity and geography of soil fungi. Science 346 (6213). https://doi.org/10.1126/science.1256688.

Terrer, C., et al., 2016. Mycorrhizal association as a primary control of the CO 2 fertilization effect. Science 353 (6294), 72–74. https://doi.org/10.1126/science.aaf4610.

Thessen, A., 2016. Adoption of Machine Learning Techniques in Ecology and Earth Science. One Ecosystem 1, e8621. https://doi.org/10.3897/oneeco.1.e8621.

Thomas, P., Büntgen, U., 2019. A risk assessment of Europe's black truffle sector under predicted climate change. Sci. Total Environ. 655, 27–34. https://doi.org/10.1016/j.scitotenv.2018.11.252.

Wright, M.N., Ziegler, A., 2017. Ranger : a Fast Implementation of Random Forests for High Dimensional Data in C++ and R. J Stat Softw 77 (1). https://doi.org/10.18637/jss.v077.i01.