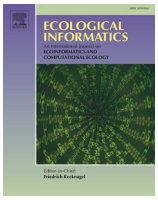
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Analysis of climate change impacts on the biogeographical patterns of species-specific productivity of socioeconomically important edible fungi in Mediterranean forest ecosystems

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ABSTRACT

In Mediterranean forests, many species of fungi produce fruiting bodies every autumn, some of which are of great social and economic interest as NTFPs. In addition, these fungi are an essential part of the biodiversity network that ensures the proper functioning of natural ecosystems and that is currently in check due to global change. Therefore, understanding the biogeographic patterns of species-specific fungal productivity is fundamental to anticipate possible changes in the socioeconomic value of our forests and to understand the role they play in the functioning of ecosystems in terms of mitigation and adaptation to climate change. In this study we estimate the future impact of climate change (in Catalonia region, between 2023 and 2100) on five fungal species with high socioeconomic interest in a broad bioclimatic gradient representative of the Mediterranean basin using high resolution at the landscape scale. To achieve this, we use predictive models based on machine learning algorithms and a fungal database resulting from the sampling of more than 100 permanent sampling plots over 20 years. We estimate that current and future productivity patterns differ among species, under different climate change scenarios and bioclimatic regions. Our results suggest that optimal productivity areas may be shifted to higher elevations, making those species with higher productivity at higher elevations the most affected by climate change. This would mean that some species with high socioeconomic value, such as *Lactarius deliciosus* and *Boletus edulis*, could be negatively affected in their total productivity in the study area. This study highlights the need to anticipate the potential effects of climate change on fungal productivity and in particular on high socioeconomic value species and to develop management policies oriented to maintain the important role of fungi in natural ecosystems.

1. Introduction

Wild edible mushrooms play an essential role in forest ecosystem functioning and are recognized globally for their commercial and socioeconomic value as a non-timber forest products (NTFPs) (Boa, 2004; Schoenenberger-Arnaiz et al., 2017). Much of the value of NTFPs come from continuous annual returns as opposed to the intermittent returns from timber harvesting (Singh et al., 2020), and managing forests effectively for these resources can be highly beneficial for rural economies. Many traditional activities that acquire revenue from forests, such as logging and grazing, have decreased, whereas revenue from NTFPs such as mushrooms has increased (Pettenella et al., 2007). Given that the value of marketed fungi in a forest can often surpass the value of timber (Palahí et al., 2009), as well as the growing interest in edible fungi foraging recreation and tourism (Bonet et al., 2014; Mogas et al., 2005) and the revenue that can be gained from mushroom picking licenses (Pettenella et al., 2007), there is a vested interest in quantifying and evaluating this ephemeral forest product and integrating the value of edible fungi into forest planning decisions (De-Miguel et al., 2014; Martínez-Peña et al., 2012). In the study area (Catalonia region), it is

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estimated that annually 1.2 million people go at least once a year to collect mushrooms and that in the central market of Mercabarna (the most important wild edible mushroom market in Spain according to (Bonet et al., 2008)) more than 700 t of mushrooms are marketed with an average price of 10.7 €·kg^{-1} (3–17.7 €·kg^{-1}) (CEO, 2014). This denotes the great socioeconomic importance of mushrooms in Mediterranean society (Martínez de Aragón et al., 2011) and supports that changes in mushroom fruiting patterns will directly affect our society. In this regard, understanding species-specific distribution patterns is fundamental for appropriate resource management (Ehrlén and Morris, 2015) since spatial distribution patterns are intrinsically linked to species' ecology, and understanding these patterns is key to inform conservation and management decisions (Guisan et al., 2013). Besides the ecosystem services related to the social and economic valuation of mushrooms, fungi are also responsible for many of the processes occurring in ecosystems. Mycorrhizal species are important for the availability of nutrients and water for host trees (Brunner, 2001; Guidot et al., 2003; Hartnett and Wilson, 2002; Smith and Read, 2008). They aid in seedling establishment and in the provision and recycling of soil nutrients (Egli, 2011; van der Heijden et al., 2015). Additionally, they protect host plants from soil pathogens and environmental extremes (Smith and Read, 2008), and play a key role in carbon sequestration in both soil and trees (Egli, 2011; Treseder and Allen, 2000). On the other hand, saprophytic fungi obtain carbon by degrading soil organic matter, precipitating a massive release of CO_2 (Boddy et al., 2007; Rayner and Boddy, 1988).

Fungal fruiting is largely dependent on weather and climatic conditions (Bonet et al., 2010; Collado et al., 2019; Karavani et al., 2018; Morera et al., 2021; Ponce et al., 2022; Taye et al., 2016) often resulting in significant interannual variation in fungal productivity. Boddy et al. (2014), in their literature review, highlight temperature and precipitation as the most important determinants of mushroom production, although other possible factors have often been ignored. Within the global change context, this further increases the uncertainty about future provisioning of socioeconomically important fungal species and NTFPs given that climate change impacts ecosystem functioning (Kröel-Dulay et al., 2015; Menzel and Fabian, 1999) and fungal ecology (Diez et al., 2013; Kauserud et al., 2008; Morera et al., 2022; Steidinger et al., 2020). The generalized increase in temperature and the changes in the precipitation regime have varying effects on the fungal productivity of different functional groups (Morera et al., 2022) and species-specific phenology (Diez et al., 2013), so it is likely that the individual mushroom species' productivity will also have differing responses to climate change (Suz et al., 2015). Understanding the climate change impact on species-specific edible wild mushrooms gives further relevant insights into the potential changes in the socioeconomic value of forests (Ágreda et al., 2016; Büntgen et al., 2011, 2012; Steidinger et al., 2020). Additionally, it provides knowledge on forest ecosystem functioning in terms of both climate change mitigation and adaptation given fungi play a key role in forest dynamics (Mohan et al., 2014; Stokland et al., 2012).

Extensive research has been conducted to investigate the factors that influence fungal productivity. It has been demonstrated that fungal productivity is affected not only by meteorological variables, but also stand structure variables such as canopy cover (Tomao et al., 2017), basal area (Bonet et al., 2010; De-Miguel et al., 2014; Pilz and Molina, 2002) and annual tree growth (Collado et al., 2018), as well as physiological variables such as soil pH (Gassibe et al., 2015). However, few studies have focused on species-specific mushrooms with high sociocultural and economic value, and even fewer have attempted to estimate the species-specific productivity on a broad spatiotemporal scale. Given that fungal productivity in Mediterranean ecosystems is closely related to a large number of environmental drivers and that these relationships can become complex or even appear stochastic, advanced analytical methods and modeling tools are needed to deal with these challenges (Tan et al., 2006). Over the past years, the field of artificial intelligence and machine learning has enabled significant advances in the field of ecological informatics (Borowiec et al., 2022; Tuia et al., 2022; Christin et al., 2019; Wäldchen and Mäder, 2018) and promises to continue to make further progress (Morera, 2024). These techniques have allowed to improve the accuracy of results compared to more traditional modeling techniques due to the possibility to approximate non-linear relationships and to consider a large number of predictors (Meyer et al., 2019). Machine learning in ecology has been used for instance to study species distribution (Liang et al., 2022; Bellin et al., 2022), species identification through imagery (Gao et al., 2024), characterization of land use change (Gelabert et al., 2021), identification of conservable or restorable areas (Cheng et al., 2018), biodiversity conservation and estimation (Tuia et al., 2022; Chang, 2023), and invasive species risk assessment (Jensen et al., 2020).

In this study, we estimate for the first time the impacts of climate change, across a broad bioclimatic gradient and in a spatially explicit way, on the productivity of five socio-economically important fungal species, namely *Boletus edulis*, *Lactarius deliciosus*, *Tricholoma portentosum*, *Hydnum repandum* and *Macrolepiota procera*, under different climate change scenarios. To achieve the main objective, secondary objectives emerged, namely, to establish the relationships between the productivity of specific fungal species and weather conditions, and to estimate the current biogeographical patterns of the five selected fungal species. Five main hypotheses emerged from the objectives: (1) we expect different current biogeographical patterns of productivity for the different species studied and (2) a specific climate change impact on each of them, (3) Spatial and/or temporal differences in both current and climate change-induced biogeographic patterns in fungal productivity will be heterogeneously distributed throughout the landscape as a result of fine-grained spatiotemporal variations in current and future climatic conditions. Because climate change will lead to a greater change in meteorological conditions at higher elevations and greater under RCP 8.5 than under RCP 4.5 (Kotlarski et al., 2014), we expect that changes in fungal productivity will be greater under (4) a scenario with higher greenhouse gas emissions and (5) at higher elevations. Our results and analyses were based on state-of-art methods and random forest models, a database of more than 8500 collected fungal fruitbodies, and high-resolution historical and future meteorological information to obtain spatially explicit estimates and forecasts of mushroom productivity in a wide and representative bioclimatic range of the Mediterranean forest ecosystems. To our knowledge, this is the most extensive database of macrofungal productivity in the world.

2. Materials and methods

2.1. Study area and sampling design

The study area is located in the Catalonia region, in the western Mediterranean basin. A network of 130 permanent sampling plots (10 × 10 m) extending across the pine-forested bioclimatic regions of Catalonia was used for this study namely subalpine, montane, supra- and mesomediterranean, which correspond to some of the most representative bioclimatic regions of the Mediterranean basin (Fig. 1).

Mycorrhizal species, namely, *Boletus edulis*, *Hydnum repandum*, *Lactarius deliciosus*, and *Tricholoma portentosum,* and saprotrophic species, namely, *Macrolepiota procera,* sporocarps were selected for their socioeconomic interest within the study region. *B. edulis* is considered the most relevant mushroom for international trade while L. *deliciosus* is also one of the most coveted species for both recreational pickers and trade in the study area (Martínez de Aragón et al., 2011; Voces et al., 2012). In addition, *T. portentosum*, *H. repandum* and *M. procera* are also mushrooms with a high socioeconomic value. These selected study species represent a set of species with phenological variability within the study region and that belong to both mycorrhizal and saprotrophic fungi trophic guilds.

Each mushroom of the selected fungi species was collected weekly and weighted from sample plots during the main fruiting season (July

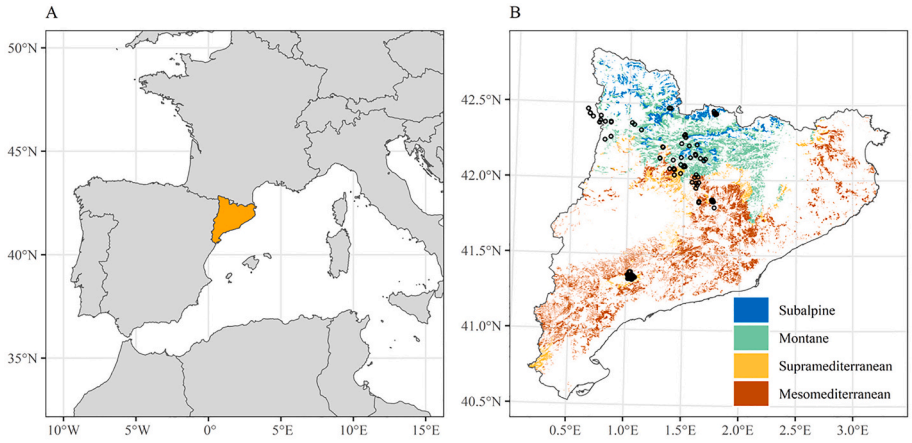


Fig. 1. Study area and sampled plots. (A) Study area (orange) location within a view of the western Mediterranean basin. (B) Pine forests of the study region and the distribution of the sampling plots. Plots outside the sampling area were taken into account due to the similarity of climatic conditions and the valuable information they provide.

through December) from 1997 to 2022 (Fig. 2). Fresh biomass production was aggregated to an annual basis and reported for each species (Table S1) since fresh biomass is how mushrooms are commonly sold in the study region. More information on sampling methods can be found in Martínez de Aragón et al. (2007).

2.2. Modeling

We trained productivity models for *B. edulis*, *H. repandum*, *L. deliciosus*, *M. procera* and *T. portentosum* based on the random forest algorithm and the R package "ranger" (Wright and Ziegler, 2017). Random forest models allow us to find consistent nonlinear ecological relationships among a large number of predictors, making them suitable for predicting this resource that sometimes appears to be driven by stochastic processes. Each model was trained to predict annual and per hectare mushroom productivity depending on August to November monthly precipitation and August to November monthly mean maximum temperature. Meteorological information resulted from monthly aggregation of interpolated and altitudinal corrected daily data, using the R package "meteoland" (De Cáceres et al., 2018), from the nearest Meteorological Service of Catalonia (SMC) and the Spanish Meteorological Agency (AEMET) meteorological stations (Table S2 summarizes sampled meteorological data).

Model variables were selected based on the importance given to each predictor (as represented by the mean decrease in node impurity of random forest decision trees), Spearman correlation between climatic predictors and scientific knowledge from previous research (Morera et al., 2021, 2022). We used the same optimal subset of predictors for

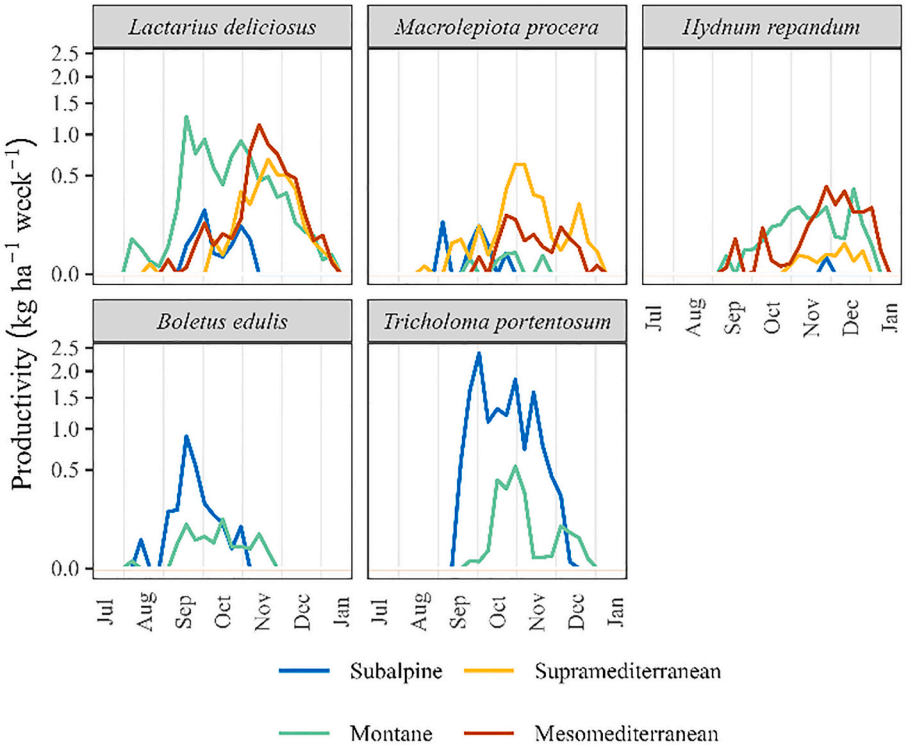


Fig. 2. Distribution of *Lactarius deliciosus*, *Macrolepiota procera*, *Hydnum repandum, Boletus edulis* and *Tricholoma portentosum* fresh productivity from July to January for the subalpine, montane, supra- and mesomediterranean bioclimatic regions. Productivity axis is shown in a square root transformation.

each species-specific model to avoid artefacts due to variable selection among fungal species. A correct selection of variables allows a better model interpretation (Coelho et al., 2019), detect problematic predictor variables (Meyer et al., 2019) and a better extrapolation in a new bioclimatic space represented by future climatic conditions (Morera et al., 2021).

Model hyperparameters were tuned for each species-specific model using Bayesian optimization focused on reducing the root mean squared error (RMSE) of the predictions based on environmental cross-validation (Roberts et al., 2017) with ten folds, as implemented in the R package "mlr3mbo" (Kotlarski et al., 2014). The search space of optimal hyperparameters was defined by the ranges of "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) shown in Table S3 (the abbreviations of the hyperparameters used correspond to the terminology used in the R package "ranger").

We evaluated trained models according to their predictive accuracy and ecological interpretation of their predictors. Environmental cross-validation with ten folds was performed to represent the new environment's predictive error accurately. Using Partial Dependence Plots (PDPs), we uncovered patterns between model predictors and species-specific productivity. The resulting PDPs were evaluated using existing scientific knowledge to determine whether the patterns found were ecologically consistent.

2.3. Estimating biogeographic patterns of current fungal productivity

Current annual productivity per hectare was estimated for each of our study species using the average climatic conditions throughout the study region pine forests over the last 30 years (1991–2022). Pine forests area (Fig. 1), namely pure stands of *Pinus halepensis*, *P. sylvestris*, *P. pinaster*, *P. nigra* and *P. uncinata* and mixed stands of *P. halepensis* and *P. nigra*, and *P. sylvestris* and *P. nigra*, were obtained from the CORINE habitat map (Moss and Wyatt, 1994). Mean climatic data were obtained at 1-km resolution from the interpolation and altitudinal correction of daily records from SCM and AEMET meteorological stations in the study area, using the R package "meteoland" (De Cáceres et al., 2018) and then aggregated at a monthly scale.

2.4. Predicting future fungal productivity under climate change

Future estimates of fungal productivity were made on the current pine forests distribution area described in Section 2.3. Due to the lack of reliable projections of forest species migration in the study area, future predictions have been made based on the current distribution of pine forests in Catalonia.

Projected daily meteorological data were obtained from the EURO-CORDEX initiative (Kotlarski et al., 2014) with an initial resolution of ~11 km. We selected simulations based on two GCMs and three RCMs, based on the criteria described by Fargeon et al. (2020) in an adjacent study region. For each GCM-RCM couple (Table S4), we compared two greenhouse gas emission scenarios, namely RCP 4.5 and RCP 8.5. Projected daily precipitation and daily mean maximum temperature were downscaled and bias-corrected to a final resolution of 1 km according to the local topography and the reference period 1990–2005. Both downscaling and bias corrections were done with the R package "meteoland" (De Cáceres et al., 2018) and the daily data were then aggregated on a monthly basis.

We predicted annual productivity (kg ha^{-1} yr^{-1}) per fungal species over 2023–2100 at 1-km resolution using monthly meteorological information. The spatially-explicit future mean trend was calculated based on the mean annual productivity of the different selected GCM-RCM couples. From there, the existence of a statistically significant monotonic trend was determined using the Mann-Kendall test (Mann, 1945), using the R package "Kendall" (McLeod, 2011). In addition, we calculated the magnitude of statistically significant linear trends using the Theil-Sen approach (Sen, 1968), carried by the R package "mblm" (Komsta, 2019). Likewise, to calculate the mean productivity of the study area and each bioclimatic region, we averaged the productivity values given by each pixel included in these areas and then used the Mann-Kendall test and the Theil-Sen approximation.

To better support the understanding of the magnitude of productivity changes we also computed the mean changes between the years 2023–2060 and 2061–2100 for those bioclimatic regions where a statistically significant change is expected according to the trend analysis explained in the previous paragraph.

3. Results

3.1. Species-specific mushroom productivity drivers and model accuracy

Species-specific models gave different importance to each main driver according to each specific fungal species (Fig. S1). Some species, i.e. L. *deliciosus*, *H. repandum* or *M. procera*, with a more widespread occurrence among the different bioclimatic regions (Fig. 3), revealed a greater similarity between individual predictors' importance. Conversely, species such as *T. portentosum* and *B. edulis*, with a restricted presence in subalpine and montane regions, showed greater variability among the predictors' importance.

Trained models showed different patterns in the relationship between productivity and environmental variables for different species and across bioclimatic regions of each species (Figs. S2 and S3). In general, PDPs revealed an increasing positive relationship between fungal productivity and precipitation for every month in each bioclimatic region, with a specific shape for each of them, largely driven by the period and region of fructification. On the other hand, the relationship between fungal productivity and the maximum temperature of each month is more blurred among the different species and bioclimatic regions. It seems to be a general pattern that a higher maximum temperature in August and September reduces fungal productivity, but for the other months, relationship between maximum temperature and productivity varies between bioclimatic regions, with a positive correlation between increased maximum temperature and productivity in the subalpine and montane regions and a negative correlation in the supra- and mesomediterranean regions. This can be clearly seen in species such as L. *deliciosus* or *H. repandum*, where mushroom productivity is spread

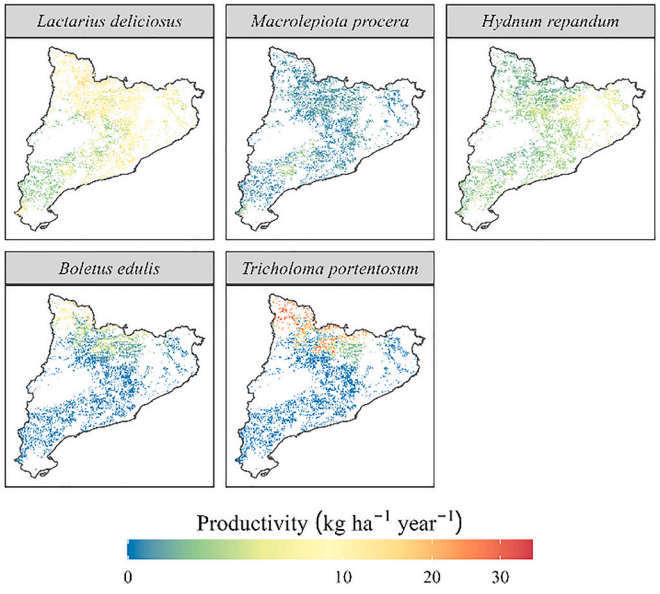


Fig. 3. Current spatially explicit productivity (fresh) of *Lactarius deliciosus*, *Macrolepiota procera*, *Hydnum repandum, Boletus edulis* and *Tricholoma portentosum*. Productivity scale is shown in a square root transformation.

across the different bioclimatic regions during most of the autumn months.

Both the prediction error and optimal hyperparameters of each species-specific model, according to an environmental cross-validation, are shown in Table S3.

3.2. Estimates of current landscape-level species-specific productivity

Among the five fungal species studied, annual productivity patterns specific to each species were observed (Figs. 3 and 4).

L. deliciosus reached its maximum productivity in the subalpine and montane region (reaching values of more than 30 kg·ha^{-1}·yr^{-1}) In addition, *L. deliciosus* stood out as the most productive species in the whole study area, with an average productivity of 5.5 kg·ha^{-1}·yr^{-1}.

T. portentosum and *B. edulis* presented a similar productivity pattern. Both species reached their maximum productivity in the subalpine region (with mean values of ~35 and ~ 15 kg·ha^{-1}·yr^{-1}, respectively), followed by the highest elevations of the montane region and with mean values close to zero productivity in supra- and mesomediterranean regions.

M. procera reached its highest productivity in the supramediterranean region (with maximum values of 8 kg·ha^{-1}·year^{-}1 and a mean of 0.4 kg·ha^{-1}·year^{-1}).

Finally, the highest productivity for *H. repandum* was predicted to occur in montane and supramediterranean areas of the northwestern part of the study region, reaching maximum values of ~8 kg·ha^{-1}·year^{-1}and a mean of ~2 kg·ha^{-1}·year^{-1}. *H. repandum* reached the lowest productivity in the subalpine zones, as well as *M. procera*.

3.3. Climate change impact on future species-specific productivity

We found differing impacts of climate change on fungal productivity depending on the fungal species at both the local scale and the bioclimatic region scale.

At bioclimatic region scale, we found that the impact of climate change will be different between species, bioclimatic regions and climate change scenarios (Fig. 5 and Table 1).

L. deliciosus was estimated to decrease in productivity in both RCP 4.5 and RCP 8.5, although under RCP 8.5 this change is predicted to occur in montane and supramediterranean areas, while under RCP 4.5 it is predicted to occur in supra- and mesomediterranean regions. It should be noted that the largest decrease would occur under RCP 8.5, with a decrease in productivity of up to 12% in the montane areas and 18% in the supramediterranean region (percentages calculated from the comparison between the average productivity between the periods 2023–2060 and 2061–2100).

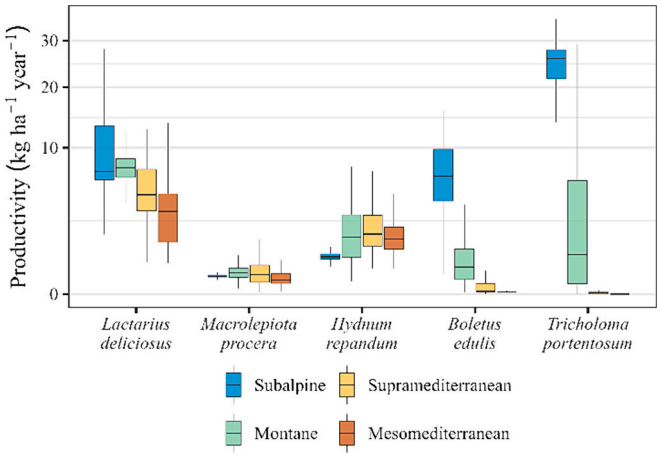


Fig. 4. Box-plot of *Lactarius deliciosus*, *Macrolepiota procera*, *Hydnum repandum*, *Boletus edulis* and *Tricholoma portentosum* current fresh productivity for the subalpine, montane, supra- and mesomediterranean bioclimatic regions. Productivity axis is shown in a square root transformation.

B. edulis and *T. portentosum* have similar productivity patterns and were similarly affected by climate change in our model. Neither species was predicted to experience changes in productivity in any of the bioclimatic regions under RCP 4.5. In contrast, both species were predicted to be significantly negatively affected in the subalpine and montane regions under RCP 8.5. In addition, *B. edulis* also estimated a 42% decrease in productivity in the supramediterranean region. *T. portentosum* decreased productivity by up to ~50% in the montane region and *B. edulis* by more than 30% in all affected bioclimatic regions.

M. procera revealed a statistically significant increase in productivity in the subalpine region under RCP 8.5, increasing up to 53%.

Like *M. procera*, we also found an increase in productivity in *H. repandum*, although with differentiated patterns across the study area between climate change scenarios. Under RCP 4.5, *H. repandum* increased productivity in all regions studied, increasing up to almost 33% in the montane region. In contrast, under RCP 8.5, productivity only increased in the subalpine and montane regions, reaching an increment of 25%.

Landscape-level results for the whole study region corroborated the results obtained for different bioclimatic regions, finding the same trends described above (more general), plus some other information at a more local scale (Fig. 6 and S4).

The predicted magnitude of the impact of climate change was not homogeneous throughout the territory or within each bioclimatic region. Within each region, we saw some variability given by the meteorological variability of each zone, more accentuated in those sites with a more changing orography (i.e., the Pyrenean mountain range). Even within the same bioclimatic region, we found areas that estimated a statistically significant positive trend and others negative (i.e., *H. repandum* in mesomediterranean forests under RCP 8.5), or areas with statistically significant changes (either positive or negative trends) and areas that did not (i.e., *L. deliciosus* in montane forests under RCP 8.5).

4. Discussion

To our knowledge, this is the first study that analyzes species-specific fungal productivity patterns of several edible fungi of high socioeconomic interest in Mediterranean areas and investigates how these patterns may be affected by climate change. Indeed, we show that climate change will affect each species differently, depending on bioclimatic regions and RCP scenarios. This provides valuable information to scientists and forest managers for the study, understanding and conservation of forest ecosystems and the ecosystem services provided by the fungi, and can be a tool for forest management decision-making in the context of climate change. Changes in fungal fruiting patterns have a direct impact on the provision of ecosystem services and the mushroom pickers distribution. This can affect the quality of the socio-cultural ecosystem service of fungi due to the collapse caused by excess pickers at certain points, increasing the nuisance of forest owners and locals (Górriz-Mifsud et al., 2017).

Biogeographic patterns of fungal productivity are very different among the studied species. Not all species fructify in the whole bioclimatic range covered by the study area, and productivity peaks are found in different bioclimatic regions for each species, which supports our first hypothesis. This is due to the individual needs of each species, although it should be further studied to which this is a result of requirements of the fungi (i.e. climate) or of the host tree (in the case of mycorrhizal fungi), as they have parallels with plants (Gill et al., 2015; Pau et al., 2011). Because of this, it is crucial to have a sufficiently extensive database to model and predict over a wide bioclimatic range (Hao et al., 2020). For this purpose, we used the world's most extensive spatio-temporal database of fungal productivity at the species-specific level based on the systematic sampling and identification of more than one hundred permanent sample plots.

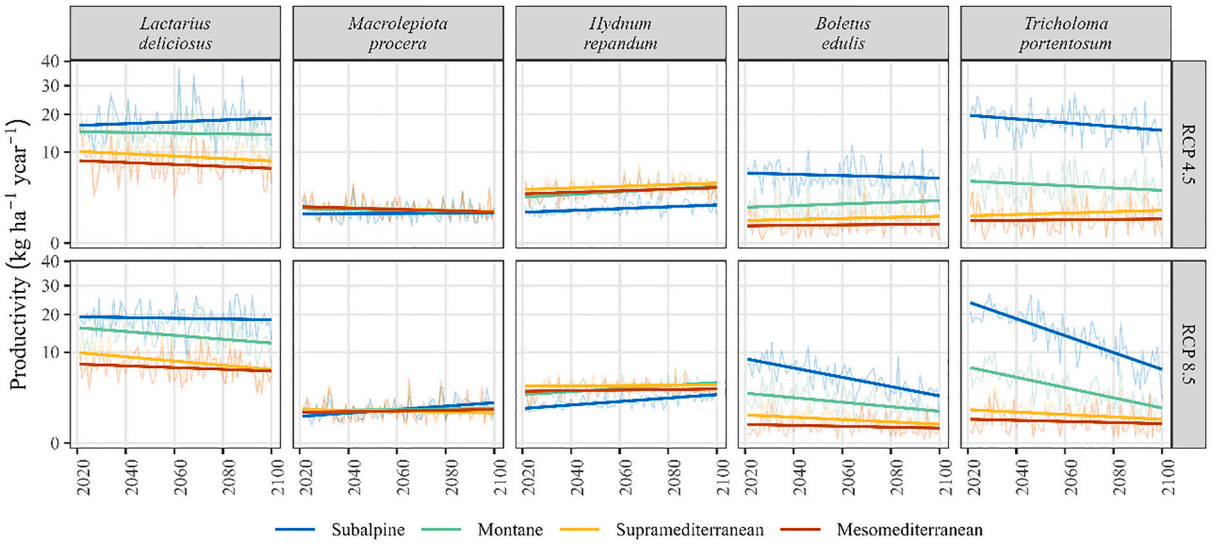


Fig. 5. Mean *Lactarius deliciosus*, *Macrolepiota procera*, *Hydnum repandum*, *Boletus edulis* and *Tricholoma portentosum* fresh productivity trend across bioclimatic regions. Future RCP 4.5 and 8.5 projections were obtained by averaging the spatially explicit fungal productivity over each of GCM-RCM couples. Straight lines show the linear trend.

Table 1
Fresh productivity changes for each specie, bioclimatic region and climate change scenario. NA represent no statistically significant changes. Percentages show productivity differences between the periods 2023–2061 and 2061 and 2100.

Fungi specie	Bioclimatic region	RCP 4.5	RCP 8.5
Lactarius deliciosus	Subalpine	NA	NA
	Montane	NA	−0.06 (12%)
	Supramediterranean	NA	−0.04 (18%)
	Mesomediterranean	NA	NA
Macrolepiota procera	Subalpine	NA	0.02 (53%)
	Montane	NA	NA
	Supramediterranean	NA	NA
	Mesomediterranean	NA	NA
Boletus edulis	Subalpine	NA	−0.07 (42%)
	Montane	NA	−0.02 (35%)
	Supramediterranean	NA	−0.01 (30%)
	Mesomediterranean	NA	NA
Tricholoma portentosum	Subalpine	−0.04 (7%)	−0.22 (45%)
	Montane	NA	−0.07 (52%)
	Supramediterranean	NA	−0.01 (24%)
	Mesomediterranean	NA	NA
Hydnum repandum	Subalpine	0.01 (34%)	0.02 (40%)
	Montane	0.02 (33%)	0.02 (25%)
	Supramediterranean	0.01 (20%)	NA
	Mesomediterranean	0.01 (21%)	NA

The patterns found by random forest models are informative about the relationships between species-specific productivity and environmental conditions. These models have been extensively contrasted to explain relationships between variables and estimate their importance (Gregorutti et al., 2017), and used in different fields of ecology, for instance biomass quantification (Kaveh et al., 2023), species distribution modeling (Valavi et al., 2021) and genomic studies (Brieuc et al., 2018). Although machine learning models cannot explicitly detect proximate variables that reveal the causal relationships between fungal productivity and the sampled environment, they can be very helpful in disentangling these complex relationships (Archer and Kimes, 2008). This is especially helpful in Mediterranean environments, where mushroom productivity is closely related to short-term weather conditions (Alday et al., 2017; Garcia-Barreda et al., 2020; Karavani et al., 2018; Morera et al., 2021), because using models able to handle a large number of predictors allows for much more accurate model fitting. However, careful selection of model variables is necessary to achieve accurate estimates (Hanberry, 2024). In addition, the large bioclimatic range over which the set of plots was sampled allowed us to capture species-specific patterns for a wide range of meteorological conditions and consequently for a wide bioclimatic area in which to predict. While this modeling technique contrasts with others used to date to predict fungal productivity (De-Miguel et al., 2014; Garcia-Barreda et al., 2020; Sánchez-González et al., 2019), according to Morera et al. (2021) it substantially improves predictions. This study also serves as a model for estimating the distribution of specific species of macrofungi from their fruiting bodies, which have been little studied to date. Despite the widespread use of this type of model, standardization and documentation of proprietary modeling protocols for different species groups remain limited (Zurell et al., 2020). Even though the use of macrofungal fruiting records has some direct advantages over other species distribution estimation methods, namely, estimation of abundance in absolute terms, phenological information and provision of ecosystem services, combining these studies with macrofungal species distribution studies using DNA sequencing (Steidinger et al., 2020; van Nuland et al., 2023) may be of great interest (Bush et al., 2017).

This study adds additional information to the spatially-explicit patterns found by Morera et al. (2021) and De-Miguel et al. (2014), in the same study region, where it was found that the highest productivity of total fungi, edible and marketable species is placed in the subalpine and montane regions. Our findings show that the spatially explicit patterns of different species can widely change within the same region. Differences in the socio-economic value associated with each species warn that species-specific studies are needed to develop conservation and management policies involving edible mushrooms.

Although the impact of climate change on the studied fungal species is unique and changing across the landscape (supporting our second and fifth hypothesis), they show some common patterns:

(1) Species with restricted fruiting at higher elevations (i.e., *B. edulis* and *T. portentosum* in the subalpine and montane regions) will be negatively affected in their current fruiting zone. This may be because these species fruit only under the cooler conditions of the study region, so that an increase in temperature would make these areas no longer suitable, or less suitable, for fruiting, which supports our fourth hypothesis.

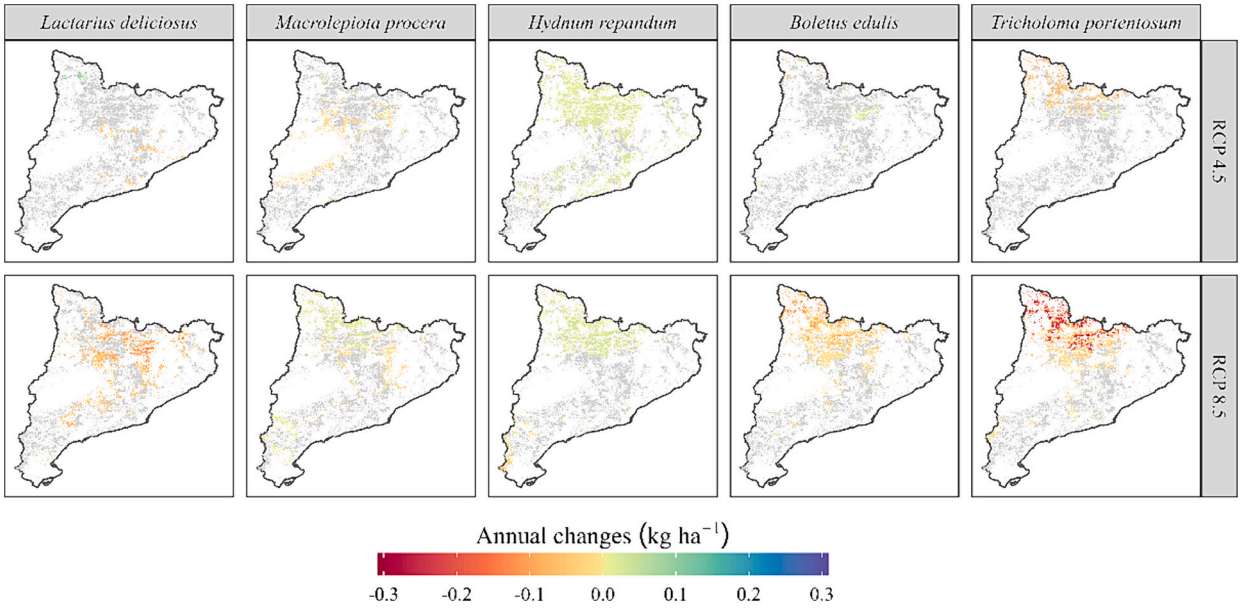


Fig. 6. Spatially-explicit expected changes in fungal fresh productivity for *Lactarius deliciosus*, *Macrolepiota procera*, *Hydnum repandum, Boletus edulis*, and *Tricholoma portentosum* species. Future RCP 4.5 and 8.5 projections were obtained by averaging the spatially explicit fungal productivity over each of GCM-RCM couples. Grey areas represent no statistically significant changes.

(2) In general, the impact of climate change on mushroom productivity will be higher under RCP 8.5 than RCP 4.5. This is in agreement with the results obtained by Morera et al. (2022) for the total wild fungi, with Karavani et al. (2018) for the total marketable wild fungi and with Thomas and Büntgen (2019) for the black truffle (*Tuber melanosporum*). This suggests that by reducing greenhouse gas emissions, it is possible to mitigate the effect of climate change on mushroom productivity. This supports our third hypothesis.

(3) Species with fruiting at intermediate elevations (i.e., *M. procera* and *H. repandum*) could see increased productivity at higher elevations. This was most clearly seen in RCP 8.5. The increase in temperature (higher in RCP 8.5) could shift optimal fruiting areas to higher elevations.

These three points indicate that the fruiting of some fungal species will move to higher elevations, which may reduce the productivity at lower elevations. And they agree with other studies focusing on specific fungal species that also reported climate change impacts on their productivity (Ágreda et al., 2016; Baragatti et al., 2019; Steidinger et al., 2020). Other studies such as Andrew et al. (2018) indicate that the fruiting period could shift forward in time but do not indicate whether this would affect total productivity. Joint studies that consider phenology and fungal productivity patterns are needed further to clarify the impact of climate change on fungi.

Some patterns found in some species are not strictly limited to these three points. For example, *L. deliciosus*, with maximum productivity in the montane and subalpine region, does not seem to be as affected by the impact of climate change in these areas of maximum productivity (only in the lower elevations of the montane region under RCP 8.5). This may be because these conditions will continue to be favorable for its development since its fruiting extends over a wider bioclimatic range and is not as specific as in other species (i.e., *B. edulis* and *T. portentosum*). Nevertheless, the fruiting of L. *deliciosus* at lower altitudes, where its productivity is significantly reduced (and presumably approaching its ecological limit), will experience a clear decrease in productivity.

Considering the varying ecological requirements of different fungal species, it becomes evident that the impacts of climate change will differ among them (Ágreda et al., 2016). Even species within the same genus, but with distinct ecological needs, could experience disparate effects, as seen for different truffle species in the Czech Republic (Čejka et al., 2020). Consequently, comprehensive investigations of each species are necessary to understand their ecology and to conduct proper socioeconomic assessments of their respective contributions to forest ecosystem services (Bonet et al., 2008).

These types of studies may have different points of interest in terms of socioeconomic considerations. Knowing the areas of greatest fruiting can be a tool for forest managers and policymakers to highlight the importance of edible mushrooms and generate opportunities to create profitable activities in rural areas (Bonet et al., 2014). The understanding that highly valuable species such as L. *deliciosus* and *B. edulis* will decrease their productivity considerably in climate change scenarios may alert us to the need to develop forest management strategies that work to maintain the important role of edible mushrooms in the supply of both cultural and provisioning ecosystem services. In addition, information on the productivity of mushrooms (supply) is a complementary tool to studies of the demand for these products (Voces et al., 2012), so understanding how the supply of individual mushroom species will change under climate change scenarios is crucial in planning for the future of this important market.

This study has not considered the migration of forest tree species or changes in land use because of the lack of consistent projections in the study region. Due to climate change, current forests could colonize new areas or disappear from some areas where they are currently found (Benito Garzón et al., 2008), modifying future mushroom fruiting patterns. In the case of fungal species that fruit at higher altitudes and that would be negatively affected in these areas in the context of climate change, they could benefit (finding their optimal fruiting) in the new forests formed at higher altitudes. In this regard, future research in this line could be complementary and very valuable. This study not only aims to directly address the impact of climate change on the biogeographic patterns of macro-fungi, but also contributes another piece to the comprehensive understanding of the functioning of Mediterranean forest ecosystems and their biodiversity. Many ecological processes inherently operate at the species scale (Clark et al., 2011) and are complementary to others at the individual and larger scales. Quantifying the strength of species interactions is a research priority (Agrawal et al., 2007; Novak et al., 2011), and is studied with models that assume that

species and not individuals interact.

5. Conclusions

This study highlights differences in current and future productivity patterns under climate change for different socioeconomically important fungal species in Mediterranean ecosystems and across a wide bioclimatic range. Our results suggest that species with the highest fruiting at higher elevations will be negatively affected by climate change, while species fruiting at lower elevations will see their fruiting optima shifted to higher elevations. In addition, climate change could represent the loss of a high percentage of the average annual production of some fungi species with great socioeconomic interest, such as *Lactarius deliciosus* and *Boletus edulis*. The complexity of different fungal-species fruiting patterns across the territory should be highlighted due to the specific ecological requirements of each one of them that affect their productivity. We alert of the importance of anticipating the impact of climate change on the fruiting dynamics of fungi, particularly those species with a high socioeconomic value, and provide valuable knowledge to aid in the adoption of appropriate management measures to preserve the multiple ecosystem services these fungi represent.

Contributions

JMdA, JAB and Sd-M contributed in the installation of the sampling plots and data collection. AM, H.L 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.

CRediT authorship contribution statement

Albert Morera: Methodology, Validation, Supervision, Investigation, Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Hannah LeBlanc:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Juan Martínez de Aragón:** Writing – review & editing, Writing – original draft, Data curation. **José Antonio Bonet:** Writing – review & editing, Writing – original draft, Data curation. **Sergio de-Miguel:** Methodology, Validation, Supervision, Data curation, Investigation, Resources, Project administration, Funding acquisition, Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

Authors declare no conflict of interest.

Data availability

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2024.102557.

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