Effect of climatic and micro-climatic conditions on the provisioning of fungal-based ecosystem services in Mediterranean pine stands

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Abstract

Mushrooms are one of the most important non-wood forest products in the Mediterranean Basin. They provide a wide variety of ecosystem services, including a contribution to the sustainability of forest ecosystems and global carbon cycle. Moreover, wild edible species possess a strong socio-economic significance.

Climate appears to be the most important factor determining mushroom productivity. Climate change models predict drier and hotter conditions for the Mediterranean, raising the concern about the long-term provision of mushroom ecosystem services, because of the expected reduction of water availability in the soil as a result of decreased precipitation and increased evapotranspiration.

Soil moisture is assumed to be an important micro-climatic variable affecting mushroom productivity since it integrates climate, site variables and forest stand characteristics. With the aim to increase our understanding of the interaction between climate and micro-climate, and their relative role in determining mushroom occurrence and productivity, we used a long-term yield data-base from 28 permanent mushroom inventory plots established in 2008 in Pinus pinaster stands under coastal Mediterranean climate. Mushrooms were collected on a weekly basis during the autumn fruiting season and classified as total, edible and marketed mushrooms. A process-based soil water balance model was used to reconstruct soil moisture values to complement field observations. Mixed-effect two-stage models employing monthly climate and micro-climate (soil moisture) variables were fitted to mushroom occurrence and productivity data.

We found that mushroom production in the Mediterranean was primarily dependent on weather conditions during the same month, with the exception of precipitation, whose effects were found to exhibit a delay of one-month. Temperature had both positive and negative effects, with high temperatures limiting production at the beginning of the fruiting season and low temperatures limiting it at the end. Although climate-based models had better predictive power than micro-climate-based models, the latter allowed more profound insight into the processes of mushroom fruiting.

1. Introduction

Many organisms in terrestrial ecosystems are dependent on fungal communities. Indeed, mushrooms play a critical role in the sustainability of forest ecosystems and global carbon cycle (Büntgen et al., 2012; Mohan et al., 2014; Stokland et al., 2012). In particular, mycorrhizal fungi facilitate the access of plants to water and nutrients and saprotrophic fungi are key contributors to carbon and nutrient cycles. In addition, mushroom fruit bodies comprise an important part of the diet of many animal species (Boddy and Jones, 2008; Krebs et al., 2008) including humans.

Wild edible mushrooms are one of the most important non-wood forest products in the Mediterranean Basin (de Román and Boa, 2006; Martínez-Peña et al., 2012), where non-wood forest products is of particular socio-economic importance (Croitoru and Merlo, 2005; Croitoru, 2007). In many cases, the value of fungal-based ecosystem services have higher economic potential than timber-oriented forestry (Palahí et al., 2009; Pettenella and Secco, 2006). For example, in Spain, the collection and trade of wild edible mushrooms is of significant recreational and socio-economic importance, contributing to the economy of many rural communities (Bonet et al., 2014; De Frutos Madrazo et al., 2012; Martínez de Aragón et al., 2011; Voces et al., 2012).

Mushroom yield varies dramatically between years due to the variation in the environmental factors that determine the duration of fruiting season and the frequency of emergence (Boddy et al., 2014; Moore et al., 2008). Climate appears to be the foremost important environmental factor (Boddy et al., 2014; Bonet et al., 2012; Büntgen et al., 2012; Taye et al., 2016), with precipitation and temperature having major impact on mushroom phenology (Büntgen et al., 2015; Kauserud et al., 2012, 2008; Moore et al., 2008), yield (Bonet et al., 2012, 2010; Büntgen et al., 2015; Krebs et al., 2008; Ogaya and Peñuelas, 2005) and diversity (Bonet et al., 2010; Hernández-Rodríguez et al., 2015; Salerni et al., 2002) Moreover, the interaction between both variables also has significant effects. For example, recent trends of temperature increase in humid temperate regions has been found to correlate with an increased yield and earlier mushroom emergence, while a decreased and delayed production have been observed under drier Mediterranean conditions (Boddy et al., 2014).

The future drier and hotter conditions predicted by climate change models for the Mediterranean region (Allen et al., 2014) and the expected reduction in water availability and soil moisture will likely enhance drought stress in the forests (Gracia et al., 2002; Peñuelas et al., 2004), eventually affecting negatively mushroom productivity (Ágreda et al., 2015; Büntgen et al., 2015; Ogaya and Peñuelas, 2005). Therefore, the ecological and socio-economic importance of mushrooms requires a better understanding of the climatic drivers of mushroom production in order to ensure and forecast the provision of fungal-based ecosystem services, especially under the context of climate change.

Mushroom productivity is largely determined by the combination of climate, site and soil variables and forest stand characteristics (Bonet et al., 2010, 2008; De-Miguel et al., 2014). Since these three factors determine micro-climatic conditions, micro-climatic variability may be considered an integrative factor to explain the stochasticity and spatial unevenness of observed mushroom fruiting patterns. Moreover, mushroom production models considering climate variables solely may fail to capture the actual water availability in the soil as they ignore soil water fluxes, especially those driven by evapotranspiration demands (Ágreda et al., 2015). Nevertheless, long series of micro-climatic records in mushroom monitoring plots are scarce, thus most studies on mushroom productivity are usually lacking such measurements (Boddy et al., 2014), constituting a major drawback to our understanding of productivity patterns..

Models aiming at incorporating mushroom production for multi-objective management planning are in short supply, negatively affected by the lack of long-term monitoring of mushroom yield, especially in drought-prone environments such as the Mediterranean (Mohan et al., 2014). Nevertheless, the ecological and socio-economic importance of mushrooms in the Mediterranean basin, together with the current and further expected decline in productivity, makes it necessary to better understand the interaction between climatic and micro-climatic variables, and how they influence mushroom occurrence and productivity.

In this study, we aim at shading light on the climatic and micro-climatic conditions driving mushroom emergence (i.e., probability of occurrence) and mushroom productivity (i.e., yield) under typical Mediterranean conditions. Moreover, we intend to better understand the relationship between climate and micro-climate variables. Analysis was done for three mushroom categories so as to include several fungal-based ecosystem services; total mushrooms to deduce on the ecosystem functioning (i.e., regulating and supporting services), and edible and marketed mushrooms to deduce on food prevalence and socio-economic activity (i.e., provisioning and cultural). We address these issues using data from a network of mushroom productivity plots in North-East Spain, and we focus on soil moisture as a key component of micro-climatic conditions. We hypothesize that soil moisture is an important micro-climatic variable affecting mushroom productivity because it integrates climate, site and soil variables and forest stand characteristics (Barroetaveña et al., 2008; Martínez de Aragón et al., 2007; Ogaya and Peñuelas, 2005). In order to have temporal series of soil moisture of the same length as mushroom yield data, we complemented measured soil moisture values with predictions obtained using a process-based water balance model. We coupled the output, and other climatic variables, with empirical mushroom occurrence and productivity models, in order to estimate the effects of climate and micro-climate conditions on the provisioning of the aforementioned fungal-based ecosystem services.

2. Materials and Method

2.1 Study area and forest plots

The study area is located in the Natural Park of Poblet in Catalonia, North-East Spain (41° 21' 6.4728 latitude and 1° 2' 25.7496 longitude). The area is characterized by a coastal Mediterranean climate, with average annual temperature of 11.8°C, annual rainfall of 665.5 mm and a pronounced summer drought usually lasting for 3 months, extending from mid-June to mid-September (Ogaya et al., 2015). The study area contains a set of 28 permanent plots in *Pinus pinaster* stands of ages around 50 years. Plots are 100 m^2 (10 m x 10 m) in size and were established in 2008 and 2009. They strongly differ in stand structure, including tree density (446-2657 trees ha^{-1}) and basal area (20.9-81.7 m^2 ha^{-1}), but they also differ in elevation (594-1013 m.a.s.l), slope (2-13%) and aspect. Soil is siliceous and has franc-sandy texture. All trees were inventoried and measured for diameter at 1.3 m breast height (DBH).

2.2 Mushroom productivity sampling

In each plot, all mushrooms were collected on a weekly basis during the autumn fruiting season, stretching over four months from September to December between 2008 and 2015, with the majority of the yield being concentrated in October and November. Mushrooms were species-identified, counted and weighted (wet and dry weight) in the laboratory. Classifications of the total annual yield were established according to edibility and marketability categories (Table 1). Edible mushrooms represent 87% of total mushrooms, and marketed mushrooms represent 43% and 50% of total and edible mushroom production, respectively. Marketed mushrooms consist of only seven species, 80% percent of the wet weight being accounted for by *Lactarius spp.* and 13% by *Macrolepiota procera*.

Table 1. Number of species, total annual yield and the proportion of the most abundant genera and species, calculated out of the total, edible and marketed mushrooms classification.

	Total	Edible	Marketed
Total number of species	364	119	7
Total annual yield (kg ha^{-1} yr^{-1})	2278	1976	978
Dominant species (%)	*Lactarius spp*. 34	*Lactarius spp.* 39	*Lactarius spp*. 79 *Macrolepiota procera* 13

Table 2. Summary of the main data used.

Model Variables	Mean	SD	Minimum	Maximum
Total mushroom yield (kg ha^{-1} yr^{-1})	86.37	102.17	0.01	481.61
Edible mushroom yield (kg ha^{-1} yr^{-1})	74.92	97.79	0.00	459.45
Marketed mushroom yield (kg ha^{-1} yr^{-1})	37.09	72.63	0.00	452.24
Total mushroom occurrence (probability)	1.00	0.00	1.00	1.00
Edible mushroom occurrence (probability)	0.94	0.24	0.00	1.00
Marketed mushroom occurrence (probability)	0.70	0.46	0.00	1.00
August precipitation (mm)	12.45	10.92	0.00	35.28
September precipitation (mm)	49.42	32.92	0.21	111.73
October precipitation (mm)	58.13	62.39	6.88	235.37
November precipitation (mm)	101.43	74.52	0.28	208.06
September number of rainy days (days)	7.92	4.54	1.00	14.00
October number of rainy days (days)	8.00	3.36	4.00	14.00
November number of rainy days (days)	9.47	5.80	2.00	25.00
November average temperature (°C)	8.53	1.86	3.98	11.96
December average temperature (°C)	5.09	1.59	1.08	7.80
September average maximum temperature (°C)	22.33	2.90	15.37	27.71
October average maximum temperature (°C)	17.77	2.22	12.23	21.83
November average minimum temperature (°C)	4.14	1.73	0.83	7.32
December average minimum temperature (°C)	0.71	1.29	-2.68	3.03
September average relative humidity (%)	67.02	4.18	59.32	76.24
September average maximum relative humidity (%)	95.72	2.28	90.23	98.85
September soil moisture (% of field capacity)	0.48	0.12	0.24	0.81
October soil moisture (% of field capacity)	0.60	0.19	0.24	0.93

2.3 Climatic variables and soil moisture sampling

Plot-specific daily weather variables were interpolated from Spanish meteorological weather stations (2008-2011), and from both Catalan and Spanish stations (2012-2015) following the daymet methodology (Thornton and Running, 1999; Thornton et al., 2000). Precipitation, temperature (min, max and mean) and relative humidity (min, max and mean) were estimated in each plot averaging the values of several meteorological stations with weighting factors that depended on the geographic proximity to the target plot. Furthermore, the estimate from each meteorological station was corrected for differences in elevation between the station and the target plot. The high dependence of precipitation on local topography (e.g., altitude, aspect) and the distance from weather stations might result in false-predictions of rain events that have not reached the plot, or miss-predictions of rain events which occurred locally at the plot but did not reach the weather stations. This limitation affected not only the estimated probability of occurrence for rain, but also the intensity of rain events.

Volumetric soil content below-ground was measured using Decagon 5 TM probes (Decagon devices Inc., USA) in each of the 28 plots. Soil sensors were placed in the middle of each plot, 12-15 cm below-ground, and measurements were recorded every minute and stored as 2-hour average on a data logger EM50 (Decagon devices Inc., USA). Volumetric soil moisture was converted to percentage of moisture relative to field capacity using Saxton equations (Saxton et al., 1986).

2.4 Soil moisture prediction

Since soil moisture measurements had started in April 2013, they overlapped only partially with the mushroom collection period, which began earlier in 2008. To complement field observations, a process-based soil water balance model, implemented in the R package called ‘medfate’ (De Cáceres et al., 2015) was used to reconstruct the historical daily series of soil moisture. The model requires forest stand characteristics, site and soil variables and meteorological series as inputs. Each individual tree was treated separately, and its height and leaf area index were estimated from DBH according to allometric equations fitted particularly for *P. pinaster* from the Spanish Third National Forest Inventory (Villanueva, 2004). Soil was described in the model using two layers: topsoil (0 – 30 cm) and subsoil (30 – 150 cm). Soil texture was available from plot sampling. Macro-porosity was estimated from sand content and bulk density (Stolf et al., 2011), and values of the latter were obtained from the Harmonized World Soil Database (Fao/Iiasa/Isric/Isscas/Jrc, 2009). We used interpolated meteorological series as climatic input. The interpolation method proved superior compared to simple assignment of weather data from the closest station, when compared as an input for the soil moisture balance model. Since the model does not simulate changes in forest structure, to account for tree growth we simulated soil water balance twice for each stand, using DBH measurements from two inventories, one carried out in December 2010 and the other in August 2013. Model predictions for the period prior to the first inventory (i.e., 2008-2010) and after the second inventory (i.e., 2013-2015) were obtained using DBH values from the first and the second inventories, respectively. Predictions for the period between the two inventories were obtained averaging the two simulations, using weights based on their relative proximity to each of the inventories.

Top-soil moisture predictions were validated by comparing them with the field measurements based on the mean square deviation (MSD) and its decomposition into three additive components; squared bias (SB), non-unity slope (NU) and lack of correlation (LC) (Gauch et al., 2003). The comparison was done using daily and monthly time-steps.

Since model predictions are sensitive to the proportion of fine roots in each soil layer and this information was lacking, we determined the partitioning of fine roots that maximized the fit to observed soil moisture data in each plot. Specifically, 100 model simulations were done for each plot varying the root proportion in the topsoil between 0.01-0.99 (the proportion of roots in the subsoil was its complement). We selected the partitioning of fine roots corresponding to the lowest MSD between observed and predicted soil moisture. Wilcoxon tests indicated a statistically significant reduction in MSD between calibrated and non-calibrated fine root partitioning regardless of the temporal resolution of the comparison with observed data (daily, weekly and monthly time steps). Finally, a dataset of monthly averages of soil moisture was constructed, incorporating field observations complemented by model predictions for the missing period. Daily meteorological data was also aggregated into monthly values before building mushroom productivity models.

2.5 Mushroom occurrence and productivity modeling

Annual yield models were developed for the fresh mass of total, edible and marketed mushrooms, using data from the 28 mushroom inventory plots. Monthly values of the following climatic and micro-climatic variables were used as predictors of annual yield: accumulated precipitation, number of rainy days, average mean temperature, average maximum temperature, average minimum temperature, diurnal temperature difference, average mean relative humidity, average maximum relative humidity and average minimum relative humidity (Table 2).

A preliminary examination of the correlation between all monthly climatic and micro-climatic variables and the total, edible and marketed annual mushroom yield was done based on both Spearman and Pearson correlation matrices. Variables showing high correlation, as well as variables known as important predictors from the literature, were plotted against the response variables in order to evaluate the shape of their relationship. Finally, predictors were selected only if their correlation with mushroom yield was statistically significant, biologically sound and in agreement with current scientific knowledge on forest and fungal ecology, while at the same time avoiding multicollinearity.

Micro-climate refers to variables derived from the interaction between climate, site and soil variables and forest characteristics. Hence, micro-climatic variables are plot-specific. Soil moisture is representing the combined effect derived from precipitation, soil structure and texture, and forest stand characteristics. We differentiated between climate-based and micro-climate-based models by replacing precipitation (both accumulated rainfall and number of rainy days) with soil moisture values (either measured in the plots or predicted by the process-based model).

We fitted mixed-effect models (Pinheiro and Bates, 2000) using plot identity as random effect to account for between-plot differences arising from variation in site, soil and forest characteristics. Year random effects were not considered since the productivity of the same plot is mainly driven by climatic differences between years and adding a year random effect would hinder assessing the role of climatic and micro-climatic variables on mushroom productivity, which was the focus of this research.

The probability of occurrence of mushrooms in a given plot and year was 1 (i.e., for every plot, in every year, at least some mushrooms emerged). Nevertheless, when focusing on edible or marketed mushroom species zero annual yield values occurred in several plots. This pattern becomes more prominent due to the stochastic nature of mushroom emergence and the small size of inventory plots, further increasing the probability for zero yield. Therefore, a two-stage modeling approach was used for modeling annual production of edible and marketed mushrooms, accounting for two separate states (De-Miguel et al., 2014; Hamilton Jr. and Brickell, 1983). The first stage aimed at estimating the probability of mushroom emergence by means of logistic regression (Eq. 1) using a logit link function (Eq. 2) based on binomially distributed data concerning the absence or presence of mushrooms in a given plot and year. The second stage aimed at estimating mushroom yield in log scale, conditional on the former probability of occurrence, using linear mixed-effects modeling (Eq. 3). Snowdon's bias correction factor (Snowdon, 1991) was used when back-transforming model predictions from log scale to original units.

The final production models result from the multiplication of the probability of occurrence by the yield conditional on the probability of occurrence (Eq. 4), thus reflecting a combined effect of two separate states, thus revealing the distinct climatic and micro-climatic variables required by each.

Eq. (1) $$\mathrm{P}(\mathrm{y} = 1|\mathrm{x})_{ij} = \pi(\mathrm{x}) = \frac{1}{1+ e^{-[(\alpha_0+a_{0i})+\alpha X_1]}}$$

Eq. (2) $$\mathrm{g}(\mathrm{x}) = \log\left[\frac{\pi(\mathrm{x})}{1-\pi(\mathrm{x})}\right] = (\alpha_0 + a_{0i}) + \alpha X_1$$

Eq. (3) $$log(yield_c)_{ij} = (\beta_0 + b_{0i}) \ + \beta \log(X_2) + \varepsilon$$

Eq. (4) $$\mathrm{yield}_{ij} = \pi(\mathrm{x}) \times e^{\log(\mathrm{yield}_c)} \times \mathrm{Snowdon}$$

Where $\mathrm{P}(\mathrm{y} = 1|\mathrm{x})$ is the probability of edible or marketed mushroom occurrence in plot *i* and year *j*. $\log(yield_c)$ is the yield (kg ha^{-1} yr^{-1}) conditional on occurrence of edible or marketed mushroom, except for total mushroom biomass for which it represents the absolute annual yield since the occurrence of this group is always 1 in the data. yield_{ij} is the predicted total, edible or marketed mushroom yield (kg ha^{-1} yr^{-1}) in plot *i* in year *j*. α and β denote fixed-effects model parameters, a_0 and b_0 denote random effects, X_1 and X_2 are vectors of predictor variables and ε is residual following a normal distribution with mean equal to zero and variance equal to σ^2. Snowdon is the correction factor of the back-transformation bias.

Model evaluation and selection was iterative and systematic based on forward selection of predictors upon fitting statistics, considering the significance of model parameters (t-value > 2, p-value < 0.05), likelihood-ratio tests and residual standard error. Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) were used for variable selection in order to prevent over-fitting and construct parsimonious models. Logistic models for the probability of mushroom occurrence were further assessed by computing their receiver operating characteristics (ROC) curve and its corresponding area under the curve (AUC). Yield models were further evaluated by partitioning their MSD in three additive components; SB, NU and LC (Gauch et al., 2003).

All data analyses and model fitting were performed in R software 3.2.2 (R Development Core Team, 2015). Mushroom models were fitted using "glmer" and "lmer" functions of "lme4" package (Bates et al., 2014).

3. Results

3.1 Water balance model and soil moisture estimation

Soil moisture predictions of the water balance model matched reasonably well the values measured in the plots, with the single exception of plot 22, which exhibited higher MSD (Figure 1). The high bias for this particular plot was probably caused by its extreme gross texture and high rock content (which might result from an unrepresentetive soil texture) leading to very low water holding capacity and strong fluctuation of soil moisture values. Therefore, for this specific plot, we decided to discard the predicted values. The proportion of fine roots distributed between topsoil and subsoil was calibrated for each plot, reducing significantlly the MSD values. As a result, the average MSD was 0.025.

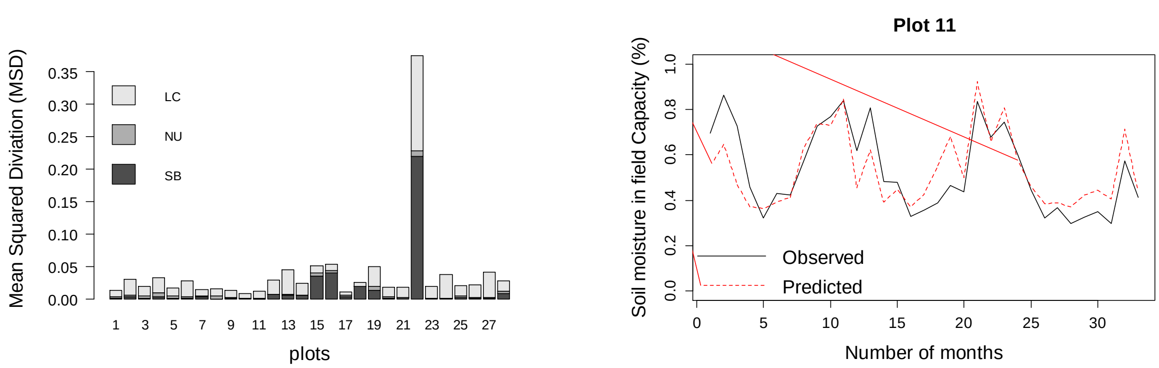

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Figure 1. a) Plot-specific mean squared deviation (MSD) of soil moisture predictions resulting from the difference between measured soil moisture values and model's predictions after calibration. The MSD is partitioned in three components; Squared Bias (SB), Non-unity Slope (NU) and Lack of Correlation (LC). b) Comparison of predicted and observed monthly soil moisture between field measurements and model prediction, an example of plot 11.

3.2 Models for total mushroom production

The information about model parameter estimates and predictors of total mushroom production (kg ha^{-1} yr^{-1}), together with the uncertainty of their estimates are presented in Table 3, while the individual effect of selected parameters is presented in Figure 2. The climate-based model (residual variance 1.031, plot random effect variance 0.330) performed better than the micro-climate-based model (residual variance 1.690, plot random effect variance 0.287), and the root mean squared deviation (RMSD) was 83.2 (kg ha^{-1} yr^{-1}) and 98.7 (kg ha^{-1} yr^{-1}), respectively. For both models SB was zero, and the majority of error was derived from LC, which was higher in the micro-climate-based model. On the other hand, NU was slightly lower in the micro-climate-based model (Figure 5).

Precipitation and temperature are the most important predictors in the climate-based model. Precipitation of September, together with the accumulated number of rainy days in September, October and November, all had a significant positive influence on the annual total mushroom yield. For each month separately, the number of rainy days were increasing with the amount of precipitation. Therefore, it often revealed as a more significant predictor, contributing additional insight into the effect of the distribution of precipitation on mushroom productivity. The combined effect of November and December's average minimum temperature had a significant positive effect on mushroom yield, meaning that the higher the minimum temperatures were the higher was the yield.

The micro-climate-based model included a wider variety of predictors as compared to the climate-based model. Total mushroom annual yield exhibit a positive correlation with soil moisture of October, the combined effect of November and December's average minimum temperature and the average maximum relative humidity of September. Furthermore, the model reveals a negative effect of the combined average maximum temperatures of September and October, meaning that the lower the maximum temperatures the higher the yield.

Table 3. Fixed parameter estimates of the models, describing the relationship between total mushroom yield and climatic and micro-climatic predictors. P 9 is the accumulated precipitation in September, raindays 9 is the number of rainy days in September when 10 and 11 represent October and November, respectively, Tmin 9/ Tmax 9 are the average minimum/maximum temperature in September when 10, 11 and 12 represent October, November and December, respectively, and RHmax 9 is the average maximum relative humidity in September, SM 10 is the average soil moisture in October. Brackets represent accumulated values.

Model	Eq.	Predictor	Coeff.	Estimate	St. error	T value
Climate-based	3	Intercept	β_0	-5.498	0.615	-8.945
		P 9	$\beta 1$	0.022	0.002	9.337
		log(raindays 9+ raindays 10+ raindays 11)	$\beta 2$	2.096	0.205	10.195
		(Tmin_11+Tmin_12)	$\beta 3$	0.259	0.029	8.791
Micro-climate-based	3	Intercept	β_0	-29.849	4.835	-6.173
		SM 10	$\beta 1$	2.536	0.600	4.224
		(Tmax 9+Tmax 10)	$\beta 2$	-0.225	0.029	-7.710
		(Tmin 11+Tmin 12)	$\beta 3$	0.445	0.046	9.634
		RHmax 9	$\beta 4$	0.403	0.058	6.939

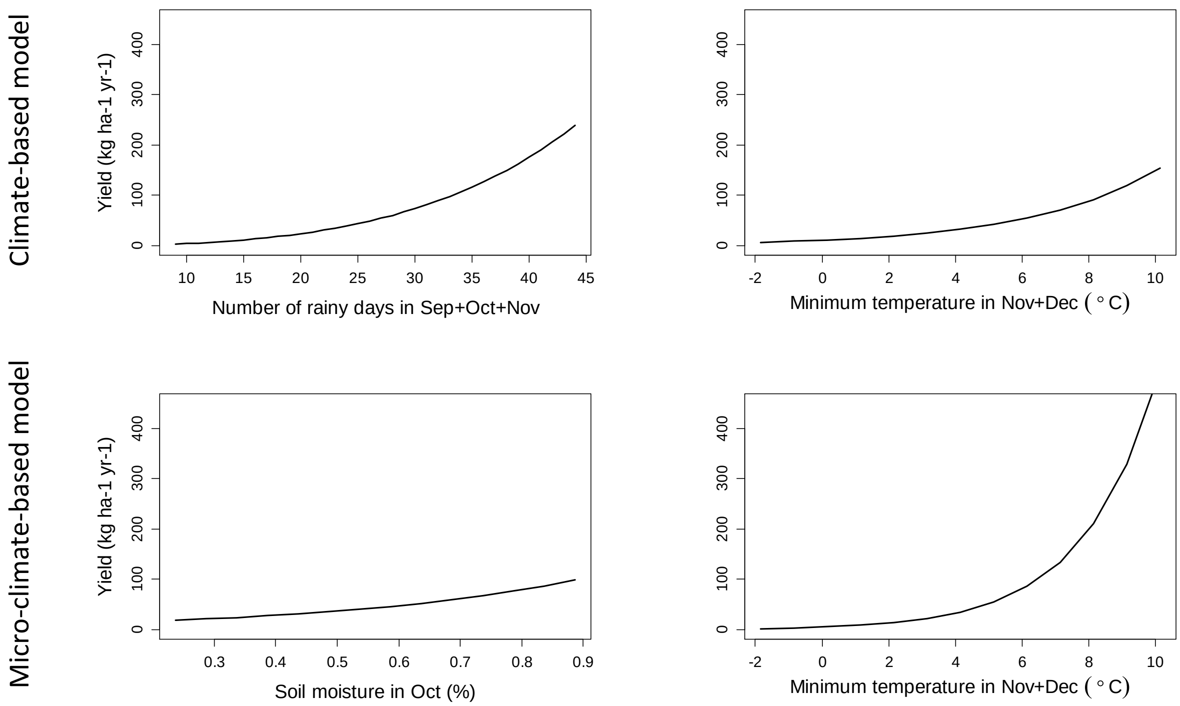

Figure 2. Effect of individual predictors on total mushroom yield, for climate-based and micro-climate-based models.

3.3 Models for edible mushroom occurrence and productivity

The information about the models of edible mushroom production (kg ha^{-1} yr^{-1}) and the uncertainty of their estimates are presented in Table 4, for both the probability of occurrence and yield conditional on occurrence (kg ha^{-1} year^{-1}). The individual effect of selected parameters is presented in Figure 3.

The probability of occurrence in the climate-based model (AUC= 0.90) was positively related to the number of rainy days in October and the combined average temperature of November and December. The yield conditional on occurrence model (residual variance 1.340, plot random effects variance 0.520) shared similar predictors with the total mushroom yield model. The root mean squared deviation (RMSD) was 85.7 (kg ha^{-1} yr^{-1}), SB was zero and the majority of error was derived from LC (Figure 5).

The probability of occurrence in the micro-climate-based model (AUC= 1.00) was positively correlated with the soil moisture in October and the combined average minimum temperature of November and December. The yield conditional on occurrence model (residual variance 1.941, plot random effects variance 0.468) differed from the total mushroom yield model only in variable transformation. Moreover, it shared similar predictors with the probability of occurrence model with the sole addition of the positive influence of maximum relative humidity of September. The root mean squared deviation

(RMSD) was 88.0 (kg ha^{-1} yr^{-1}). SB was zero, the majority of error was derived from LC, and NU was slightly lower compared to the climate-based model (Figure 5).

Table 4. Fixed parameter estimates of the models describing the relationship between edible mushroom yield and climatic and micro-climatic predictors. P 9 is the accumulated precipitation in September, raindays 9 is the number of rainy days in September when 10 and 11 represent October and November, respectively, T /Tmin 9 /Tmax 9 are the average mean/minimum/maximum temperature in September when 10, 11 and 12 represent October, November and December, respectively, and RHmax 9 is the average maximum relative humidity in September, SM 10 is the average soil moisture in October. Brackets represent accumulated values.

Model	Eq.	Predictor	Coeff	Estimate	St. error	T value	P value
Climate-based	1	Intercept	α_0	-13.135	4.188		0.002**
Logistic		Sqrt(raindays 10)	α	3.388	1.301		0.009**
		sqrt(T 11+T 12)	α	2.291	0.718		0.001**
Yield	3	Intercept	β_0	-5.828	0.842	-6.921	
		P 9	β	0.025	0.002	9.237	
		log(raindays 9+ raindays 10+ raindays 11)	β	2.031	0.260	7.794	
		(Tmin 11+Tmin 12)	β	0.269	0.037	7.251	
Micro-climate-based	1	Intercept	α_0	-17.008	12.630		0.178
Logistic		Sqrt(SM 10)	α	44.221	21.509		0.040*
		(Tmin 11+Tmin 12)	α	9.722	2.628		0.000***
Yield	3	Intercept	β_0	-184.915	28.923	-6.393	
		Sqrt(SM 10)	β	3.243	1.023	3.168	
		(Tmax_9+Tmax_10)	β	-0.235	0.034	-6.869	
		(Tmin_11+Tmin_12)	β	0.425	0.057	7.352	
		Log(RHmax_9)	β	42.313	6.593	6.417	

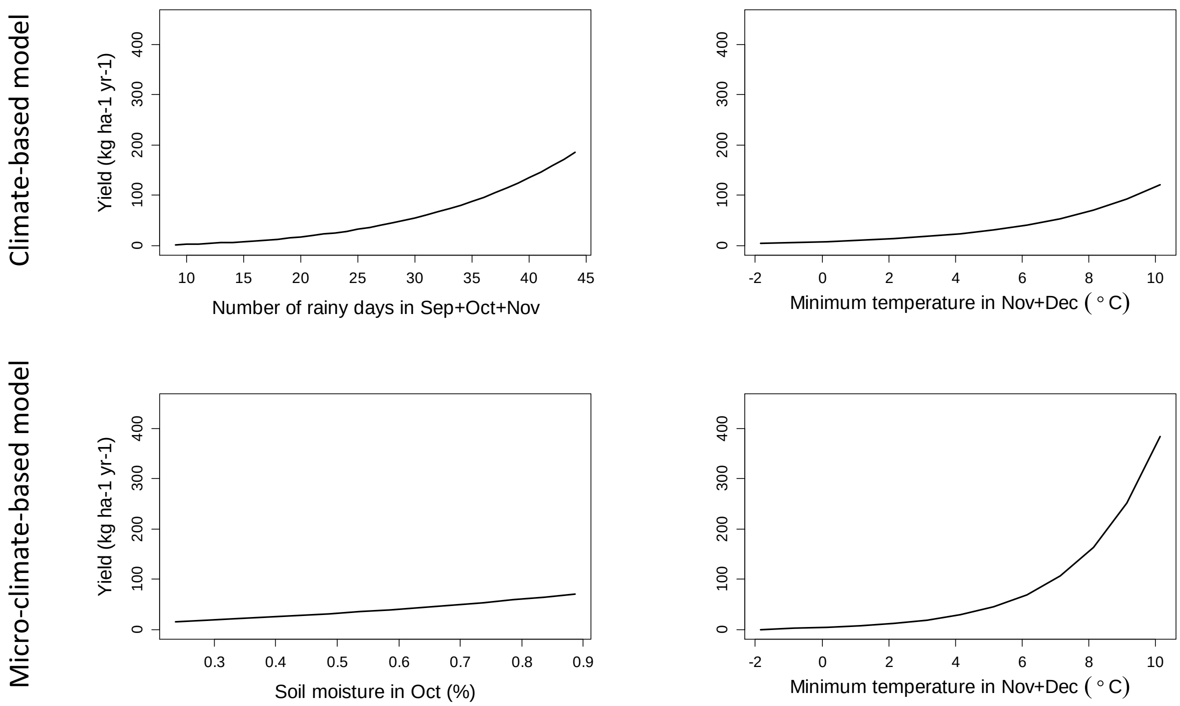

Figure 3. Effect of individual predictors on edible mushroom yield, for climate-based and micro-climate-based models.

3.4 Models for marketed mushroom occurrence and productivity

The information about the models of marketed mushroom production (kg ha^{-1} yr^{-1}) and the uncertainty of their estimates are presented in Table 5, for both the probability of occurrence and yield conditional on occurrence. The individual effect of selected parameters is presented in Figure 4. The probability of occurrence in the climate-based model (AUC = 0.96, plot random effect variance 3.419) was positively correlated with the number of rainy days in September, the amount of rain in October and the average minimum temperature of November. The yield conditional on occurrence model (residual variance 1.367, plot random effects variance 0.724) exhibited two main differences compared to the probability of occurrence model; an increasing-decreasing influence of the precipitation amount in October suggesting that extreme high values of precipitation might cause a decrease in the yield of marketed mushrooms, and a positive influence of November's mean temperature only. The root mean squared deviation (RMSD) was 51.3 (kg ha^{-1} yr^{-1}). SB was zero, NU virtually zero, while the error was almost completely derived from LC (Figure 5).

The probability of occurrence in the micro-climate-based model (AUC = 0.93) was positively influenced by the combined effect of soil moisture in September and October and the average minimum temperature of November, while negatively affected by the average maximum temperature of October. The yield conditional on occurrence model (residual variance 1.861, plot random effects variance 0.768) showed to be positively influenced by soil moisture of October and maximum average temperature of November, while negatively affected by maximum average temperature of October. The root mean squared deviation (RMSD) was 69.7 (kg ha^{-1} yr^{-1}). SB and NU were zero, while the whole error was derived from LC (Figure 5).

Table 5. Fixed parameters of the models describing the relationship between marketed mushroom yield and climatic and micro-climatic predictors. P 10 is the accumulated precipitation in October, raindays 8 is the number of rainy days in August when 9 represent September, T 11 /Tmin 11 are the average mean/minimum temperatures in November, Tmax 10 is the maximum temperature in October, and SM 9 is the average soil moisture in September when 10 represent October. Brackets represent accumulated values.

Model	Eq.	Predictor	Coeff	Estimate	St. error	T value	P value
Climate-based	1	Intercept	α_0	-7.589	1.591		0.000***
Logistic		Raindays 9	α	0.466	0.0790		0.000***
		Log(P 10)	α	1.144	0.286		0.000***
		Tmin 11	α	0.369	0.148		0.013*
Yield	3	Intercept	β_0	-9.236	1.634	-5.652	
		(raindays 8+raindays 9)	β	0.127	0.021	5.949	
		P 10	β	-0.045	0.007	-6.086	
		Sqrt(P 10)	β	1.006	0.137	7.311	
		Log(T 11)	β	2.823	0.626	4.508	
Micro-climate-based	1	Intercept	α_0	1.909	2.258		0.398
Logistic		(SM 9+SM 10)	α	6.847	1.217		0.000***
		Tmax 10	α	-0.624	0.151		0.000***
		Tmin 11	α	0.784	0.204		0.000***
Yield	3	Intercept	β_0	-3.099	2.491	-1.244	
		Log(SM 10)	β	1.859	0.446	4.169	
		Tmax 10	β	-0.285	0.127	-2.245	
		Tmax 11	β	4.839	1.661	2.913	

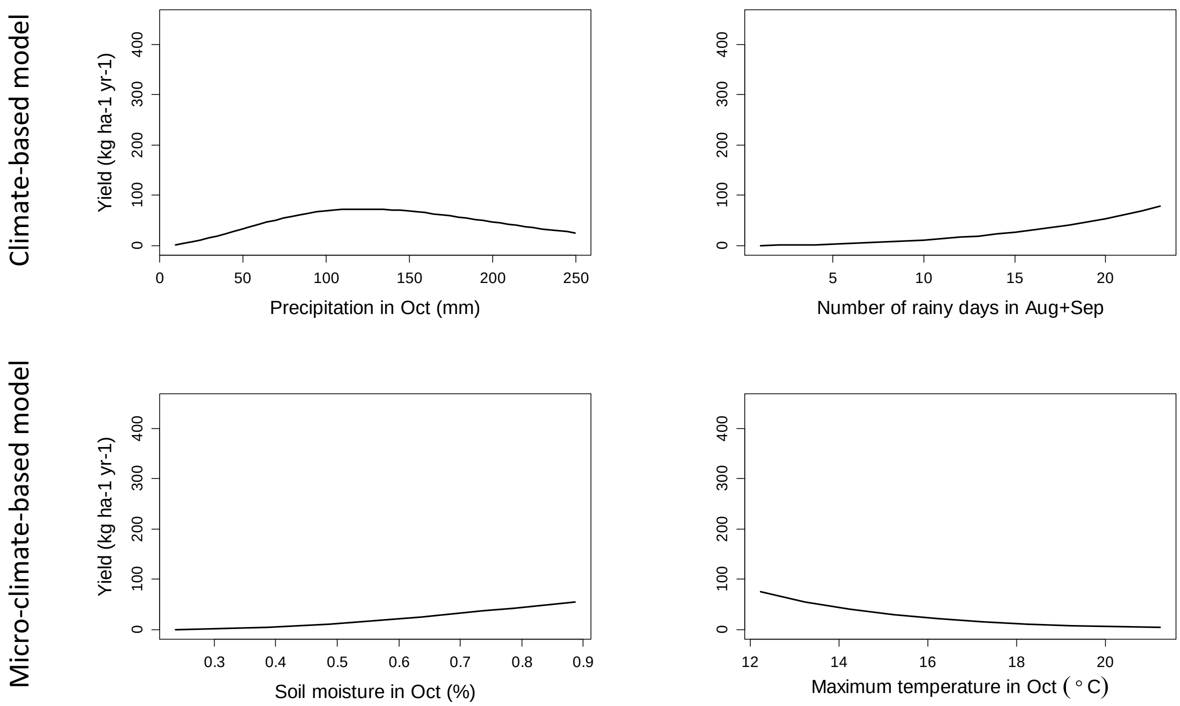

Figure 4. Effect of individual predictors on marketed mushroom yield, for climate-based and micro-climate-based models.

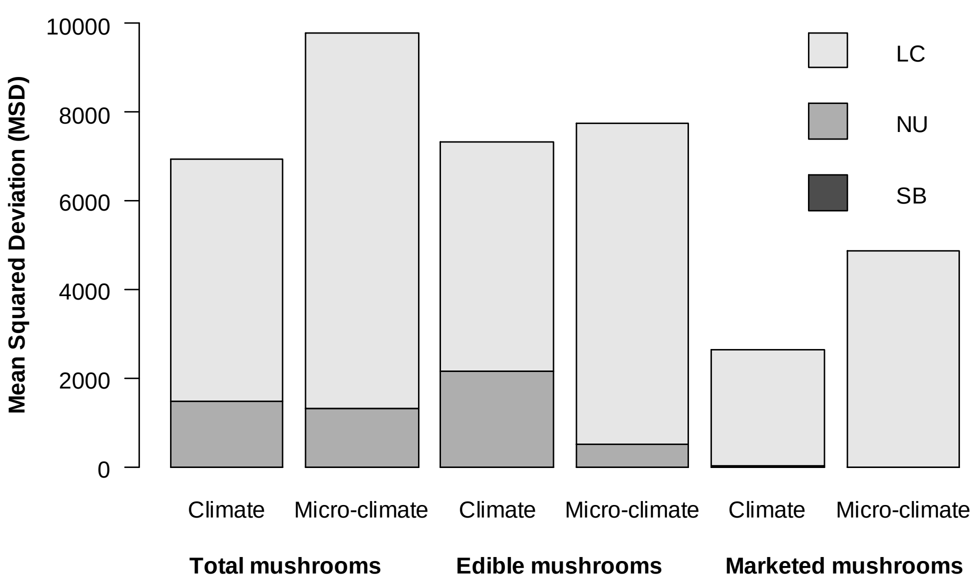

Figure 5. Mean squared deviation (MSD) of climate-based and micro-climate-based mushroom models, within the three mushroom categories, resulting from the difference between observed mushroom yield and model's predictions. The MSD is partitioned in three components; Squared Bias (SB), Non-unity Slope (NU) and Lack of Correlation (LC).

4. Discussion

4.1 Differences between yield and occurrence models and between mushroom categories

Models of total mushroom production and edible mushroom yield shared the same predictors, for both climate-based and micro-climate-based models. This result is logical since edible mushrooms represent 87% of the total mushrooms. In contrast, marketed mushrooms represent 43% of the total mushroom production consisting mainly of *Lactarius spp.* and *Macrolepiota procera*, thus those models are mainly driven by the ecological requirements of these two species, which in the wider resolution of total or edible mushroom models had a much smaller influence. The predictors composing marketed mushroom models shifted one month earlier compared with total and edible mushroom models. Namely, the climate-based model included August's precipitation and excluded November's, while the micro-climate-based model included the soil moisture of September in addition to October's. Furthermore, both excluded the temperatures in December, being the last month of the fruiting season. These results indicate on an earlier phenology of the marketed species and match the fact that *Macrolepiota procera* fruit early in the season and is exclusively responsible for the yield of September in our study area. This raises concerns regarding the future economic activity surrounding mushroom picking and trade, since edible mushrooms in Mediterranean ecosystems may be experiencing a sharp drought-induced decrease in fruit body productivity due to delayed phenology in the autumn season (Büntgen et al., 2015), while some of the earliest species to fruit belong to the marketed mushroom category.

Models for probability of occurrence and models for yield differed in their predictors. Generally, yield models consisted of a larger number of predictors which covered the extent of the whole fruiting season, while only a narrower time frame was required for the occurrence of mushrooms. For instance, the climate-based model for edible mushroom occurrence was dependent on the precipitation in October and the temperature in November and December, while the increase in yield depended on the extension of precipitation predictors throughout the fruiting season from September to November. Similarly, the micro-climate-based model depended on soil moisture in October and temperature in November and December, whereas the yield increased with the extension of convenient temperatures throughout the whole fruiting season as indicated by the addition of a negative correlation with maximum average temperature in September and October as well as a positive correlation with relative humidity in September.

Regarding marketed mushrooms, the climate-based model for the probability of mushroom occurrence showed a dependence on the precipitation in September and October and the temperature in November, while an increase in yield resulted from the addition of precipitation of August which is positively affecting the early yield of *Macrolepiota procera* in September. Another interesting difference was the increasing-decreasing effect of precipitation in October only in the yield model. This suggests that while precipitation is essential for mushroom occurrence, the effect on the yield can turn negative in excessive wet conditions (Boddy et al., 2014) which may be due to reduced soil aeration (Moore et al., 2008).

4.2 Effect of climatic and micro-climatic variables on mushroom occurrence and productivity

Precipitation and temperature are the most important predictors of mushroom emergence and yield. In the Mediterranean, mushroom production is limited in the beginning of the season (September-October) by high temperatures and low rainfall, in other words, by a prolongation of summer drought. The extension of summer-like weather during the fruiting season diminishes the production because the required autumn weather conditions are absent. Fungal communities in Mediterranean ecosystems may already be experiencing a delayed phenology and reduced production for these exact reasons (Boddy et al., 2014). On the other hand, in the end of the season (November-December), when precipitation and water availability in the soil are sufficient for mushroom fruiting, the production is limited by low temperatures. Hence, cold temperatures in these months mark an influence of winter-like weather in the fruiting season and the consequent decrease in production, as was already documented in a sub-Mediterranean climate (Hernández-Rodríguez et al., 2015). While the effect of temperature on mushroom production in the literature is reported as variable (Boddy et al., 2014), we found that there is no contradiction in having both positive and negative effects within the same ecosystem during a single fruiting season.

Interestingly, in most cases our models indicated that the average maximum and minimum temperatures for September-October and November-December, respectively, are more significant predictors than mean temperatures. While agreeing with the literature regarding a non-linear effect of temperature on fungal development (Boddy et al., 2014), these findings also propose a greater sensitivity of mushroom fruiting to daily extreme temperatures over mean temperatures, suggesting that exposure to extreme weather events might result in a greater inhibition of production.

The number of rainy days in a particular month was highly correlated with the amount of rainfall, thus in many cases revealed as a more significant predictor since it is an indicator of both a higher amount of rainfall as well as its broader distribution. Precipitation (i.e., rainfall and number of rainy days) exhibits a one-month time lag in its correlation with mushroom productivity. In all models it became a significant factor one month before the mushroom season starts (i.e., one month before September concerning marketed mushrooms and October concerning edible and total mushrooms), and ceased to be significant one month before the end of the season (i.e., one month before November concerning marketed mushrooms and December concerning edible and total mushrooms). This is in agreement with previous research indicating a one month delay in the effect of rain events on mushroom production in the Mediterranean (Bonet et al., 2012, 2010; Martínez de Aragón et al., 2007; Martínez-Peña et al., 2012; Salerni et al., 2002; Taye et al., 2016), as well as confirming expert knowledge of experienced mushroom pickers.

Our data also showed an off-season effect of weather on mushroom productivity, exhibiting a highly negative relationship between precipitation in March (and to lesser extent in the whole spring) and autumn mushroom production. However, we could not find any support in the literature for such negative effect. On the other hand, spring precipitation was inversely correlated with autumn precipitation, an accepted fundamental driver of mushroom fruiting in the autumn season. Moreover, carbon from photosynthetic activity arrives to symbiotic fungi within days (Högberg et al., 2008; Leake et al., 2001). For all these reasons, we disregarded the negative effect of March precipitation as a statistical artifact rather than a true effect, further raising skepticism regarding an off-season effect on mushroom productivity.

Nevertheless, weather beyond the mushroom season can affect mushroom phenology (Boddy et al., 2014; Büntgen et al., 2015). Similarly to our findings that the invasion of summer or winter weather to the autumn months can shorten the fruiting season and limit mushroom production, the expansion of autumn weather might result in the contrary. Therefore, suitable conditions in the months adjacent to the fruiting season can extend the length of the season, consequently affecting the annual yield.

Soil moisture is known to be a crucial driver for fungal development and fruiting (Barroetaveña et al., 2008; Martínez de Aragón et al., 2007; Ogaya and Peñuelas, 2005). Nevertheless, its effect in our models was limited to rather warm months solely (September-October). During the colder months of the fruiting season (November-December), high values of soil moisture were associated with low mushroom production, not because of a true negative effect, but due to the low temperatures (which decrease soil depletion rates but also affect fruiting negatively). This interaction produced an illogical negative correlation between soil moisture and mushroom productivity.

In all our models, soil moisture appeared as a significant mushroom predictor one month later than precipitation did, matching the initiation of fruit body production (i.e., September concerning marketed mushrooms and October concerning edible and total mushrooms). Soil moisture follows rainfall event's intensity (Ogaya and Peñuelas, 2005), and showed a positive correlation with precipitation of the same and former month. Nevertheless, maximum relative humidity, and not soil moisture, appeared significant in the month prior to fruiting (probably only due to high correlation with precipitation) indicating that precipitation is probably influencing mushroom yield mainly by increasing soil moisture. The delay between precipitation and mushroom productivity might be explained by the necessity to first acquire enough fruiting potential before the initiation of fruit bodies (Krebs et al., 2008; Salerni et al., 2002).

4.3 Causal drivers vs. predictive variables of mushroom productivity

It is important to distinguish between causal drivers and predictors of mushroom productivity. Precipitation is not the most proximal causal driver of fungal development, at least compared to soil moisture, but precipitation variables proved as more significant predictors of mushroom productivity. In other words, it seems that rain events summarize several important causal drivers, such as positive influence on soil moisture and relative humidity, and negative or positive effect on temperature (which depends on the climatic conditions in a particular area and the time of the year). Micro-climate-based models, which included soil moisture instead of precipitation variables, had lower explanatory power than climate-based models, although they were less biased compared to climate-based models since most of their error resulted from the lack of correlation between observations and predictions while exhibiting lower non-unity slope (Figure 5). Nevertheless, micro-climate-based models provided a more profound insight into mushroom production dynamics. Since soil moisture did not correlate as strongly with other variables as precipitation did, model selection led to the inclusion of predictors that were not selected in the climate-based models, and sharpened the effect of others. For example, micro-climate-based models refined the negative effect of low mean temperatures in November and October, revealing the high sensitivity of edible mushroom emergence to extreme temperatures by replacing the predictor of mean temperature by minimum temperature. Similarly, the negative effect of maximum temperatures in September and October on total mushroom production, and the positive influence of relative humidity in September on total and edible mushroom yield only appeared significant when accounting for soil moisture instead of precipitation in the models. Therefore, our results suggest that the inclusion of precipitation as a predictor, while having great predictive ability, may obscure the effect of several mushroom fruiting drivers because of the correlation between precipitation and these drivers.

5. Conclusions

Yield models are affected by weather conditions extending over the whole autumn fruiting season, while only a narrower time-frame is required to ensure the occurrence of mushrooms. Our results emphasize that mushroom production during the autumn fruiting season in the Mediterranean (September-December) is primarily dependent on weather conditions during the same month, with the exception of precipitation which exhibits a delayed effect of one-month. Temperature has both positive and negative effects on mushroom production depending on the period within the fruiting season, when production is limited by high temperature at the beginning of the season (September-October) and by low temperatures towards the end (November-December). Micro-climate-based models proved useful since they provided more profound insight into the processes of mushroom fruiting, allowing us to distinguish between causal drivers and predictors of mushroom productivity, whereas climate-based models provided better explanatory power thus may be used when the aim is yield prediction.

A higher resolution analysis would be needed (e.g., daily or weekly values) to further clarify the interaction between climate and micro-climate and their effect on mushroom production. An increased temporal resolution might lead to a better performance of soil moisture over precipitation as a predictor of mushroom productivity, since it would supply an improved representation of soil water balance between rain events, which is obscured when using monthly means. Furthermore, this fine-grained analysis would allow gaining a deeper knowledge of the relationship between precipitation, soil moisture and the time-lag effect on mushroom production, while at the same time describe more precisely the effect on phenology. The use of a process-based modeling approach proved fruitful and might supply further Insight into the effect of micro-climatic conditions which can contribute to further increasing our understanding of fungal dynamics in forest ecosystems.

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