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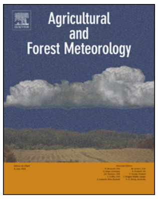

Primary productivity and climate control mushroom yields in Mediterranean pine forests

José Miguel Olano[a,*], Raquel Martínez-Rodrigo[a,b], José Miguel Altelarrea[c], Teresa Ágreda[d], Marina Fernández-Toirán[a], Ana I. García-Cervigón[e], Francisco Rodríguez-Puerta[a,b], Beatriz Águeda[a,b]

[a] EIFAB – iuFOR. Universidad de Valladolid, Campus Duques de Soria, E-42004 Soria, Spain
[b] föra forest technologies, Campus Duques de Soria, E-42004 Soria, Spain
[c] Fundación Cesefor, Calle C, E-42005 Soria, Spain
[d] Fundación Parque Científico de la Universidad de Valladolid, Campus Duques de Soria, E-42004 Soria, Spain
[e] Department of Biology and Geology, Rey Juan Carlos University. C/ Tulipán s/n, E-28933 Móstoles (Madrid), Spain

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ABSTRACT

Mushrooms play a provisioning ecosystem service as wild food. The abundance of this resource shows high annual and interannual variability, particularly in Mediterranean ecosystems. Climate conditions have been considered the main factor promoting mushroom production variability, but several evidences suggest that forest composition, age and growth play also a role.

Long-term mushroom production datasets are critical to understand the factors behind mushroom productivity. We used 22 and 24 year-long time series of mushroom production in *Pinus pinaster* and *Pinus sylvestris* forests in Central Spain to evaluate the effect of climate and forest productivity on mushroom yield. We combined climatic data (precipitation and temperature) and remote sensing data (soil moisture and the Normalized Difference Vegetation Index, NDVI, a surrogate of primary productivity) to model mushroom yields for each forest and for the main edible species of economic interest (*Boletus edulis* and *Lactarius deliciosus*).

We hypothesized that mushroom yield would be related to (i) forest primary productivity inferred from NDVI affects mushroom yields, that (ii) soil moisture inferred from remote sensors will equal the predictive power precipitation data, and that (iii) combining climatic and remote sensing will improve mushroom yield models.

We found that (i) previous year NDVI correlated (r = 0.41–0.6) with mushroom yields; (ii) soil moisture from remote sensors rivaled the predictive power of precipitation (r = 0.63–0.72); and (iii) primary production and climate variances were independent, thus the combination of climatic and remote sensing data improved models with mean R^2_{adj} as high as 0.629.

On the light of these results, we propose as a working hypothesis that mushroom production might be modelled as a two step process. Previous year primary productivity would favour resource accumulation at tree level, potentially increasing resources for mycelia growth, climatic conditions during the fruiting season control the ability of mycelia to transform available resources into fruiting bodies.

1. Introduction

Fungi play key functions in forest ecosystems. Fungi contribute to soil nutrient balance by decomposing organic matter and turning it into inorganic components that are accessible to tree roots. Mycorrhizal fungi also form symbiotic associations that increase trees rhizosphere, eventually improving water and nutrient availability, enhancing tree growth and survival and providing defense against pathogens (Allen, 1991). In addition, mushrooms play a provisioning ecosystem service as wild food that has been acknowledged for a long time across multiple cultures (Boa, 2004). The growing consideration of mushrooms as a delicatessen, with their consequent commercialization, is triggering a transformation on the alimentary sector (Zambonelli and Bonito, 2012). Mushroom supplies are mostly collected in the wild and, as a result, mushroom picking has become a popular leisure activity for urban people. In fact, the development of a mycological touristic sector is having high impact in low-populated, rural areas, contributing to diversify its economy and to expand the touristic season into the

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[*] Corresponding author.
E-mail address: josemiguel.olano@uva.es (J.M. Olano).

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mushroom fruiting season (Ágreda et al., 2014; Boa, 2004).

Mycological tourism is compromised by the existence of high uncertainty in wild mushroom yields, which impedes a stable touristic offer (Zambonelli and Bonito, 2012). This phenomenon is particularly acute in environments where climatic conditions show extreme variability among consecutive years, such as Mediterranean ones, since mushroom yields reflect inter-annual climate variations, both in terms of total production and timing of the yield season (Ágreda et al., 2015; Collado et al., 2019). Although forest management can enhance wild mushroom production by promoting tree vigor (Tomao et al., 2017), it does not diminish inter-annual variability driven by weather conditions (Ágreda et al., 2016). As a result, climate change might affect wild mushroom yields, since more intense drought events and higher evapotranspiration may play deleterious effects. However, later mushroom seasons and, particularly, more abundant spring yields due to changes in climate might provide novel windows of opportunity (Büntgen et al., 2012; Sato et al., 2012).

Developing reliable predictive models for mushroom yields is therefore a must for the expansion of this economic sector (Tomao et al., 2017). Indeed, modeling factors that determine wild mushroom yields has become an expanding area of research that benefits from the ever-growing availability of long-term data sets of mushroom yields (Alday et al., 2017; Egli et al., 2006; Fernández-Toirán et al., 2006; Herrero et al., 2019; Martínez-Peña et al., 2012). Weather conditions have been the main environmental factor considered in modeling mushroom yields, temperature being key in temperate forests (Sato et al., 2012) and precipitation in drought-limited Mediterranean environments (Ágreda et al., 2015, 2016; Alday et al., 2017; Herrero et al., 2019). Minimum temperatures can also affect mushroom yields through their effect on fruiting season length (Ágreda et al., 2015). More refined models include forest structure and tree growth rates (Bonet et al., 2008; Herrero et al., 2019), with some attempts to link mushroom yields with series of tree secondary growth (Collado et al., 2019; Primicia et al., 2016). The predictive power of these models is, however, limited and highly dependent on data collected at a local scale.

Remote sensing data have disrupted forest management by being able to monitor forest dynamics at multiple spatio-temporal scales (Barrett et al., 2016), and LiDAR techniques have been proven successful to evaluate mushrooms diversity and production (Moeslund et al., 2019; Peura et al., 2016). Soil moisture content, a critical factor for fungal growth and mushroom production (Karavani et al., 2018), can be inferred from RADAR sensors (Dorigo et al., 2017; Moran et al., 2000; Paloscia et al., 2013) with time series that are available since 1978 (Dorigo et al., 2017). In the same way, remote sensors give information about the Normalized Difference Vegetation Index (NDVI), which is a good estimator of primary productivity (Birky, 2001; Rouse et al., 1973; Wang et al., 2004a) whose interannual variations have been correlated to tree secondary growth at different spatial and temporal scales (Vicente-Serrano et al., 2016). Although preliminary attempts to correlate fungal fruiting phenology and fungal diversity to annual NDVI have been recently undertaken (Andrew et al., 2018, 2019), the relation between NDVI and fungal production has not yet been explored to the best of our knowledge, in spite of the existing well-known positive relationship between forest primary productivity and fungal yields (Ágreda et al., 2014; Alday et al., 2017; Collado et al., 2019; Herrero et al., 2019). Remote sensing data are not independent from climate, since soil moisture responds to precipitation, evapotranspiration and soil characteristics (Entekhabi et al., 1996) and climate is one of the main drivers of primary productivity in terrestrial ecosystems. Therefore, incorporating remote sensors to mushroom yields' models is a first step towards the future development of detailed predictive models, which will help to boost the mycological touristic sector at different parts of the world. At the same time, this is also an opportunity to explore more in depth the ecological role of environmental drivers on mushroom production, as well as their potential consequences on ecosystem function.

In this study, we benefited from two of the longest time series of fungal production (22 and 24 years), both collected in central Spain. We used climatic (precipitation and temperature) and remote sensing (soil moisture and NDVI) data to model total mushroom yields in wet and dry pine forests, as well as to model the production of the main species of economic interest at each forest type –*Boletus edulis* Bull. (king bolete) in wet forests and *Lactarius deliciosus* (L.) Gray (saffron milk cap) in dry forests–. Our main aim was to check whether and which of remote sensing data will allow to predict mushroom yields. Specifically, we hypothesized that (i) forest primary productivity (estimated by NDVI) will have a positive effect on mushroom yields, albeit this effect will vary depending on the trophic guild (saprophytic vs. mycorrhizal), (ii) soil moisture inferred from RADAR sensors will equal the predictive power of traditionally-used precipitation data, and (iii) the combination of climatic and remote sensing data will increase the predictive power of models for mushroom yields.

2. Material and methods

2.1. Sampling design and mushroom data

Mushroom data used in this research were collected in central Spain, in the province of Soria (Castilla y León region). Elevation ranges from 1000 m to 1200 m a.s.l. and climate is Mediterranean continental, with cold winters and a summer drought period from July to August. In this area, two pine forests dominated by *Pinus pinaster* Ait. and *Pinus sylvestris* L. were selected (Fig. 1). *Pinus pinaster* forest (dry forest, hereafter) grows over sandy soils with high permeability and low nutrient content. *Pinus sylvestris* forest (wet forest, hereafter) grows in more humid environments, over acidic soils as well but with higher nutrient content. Eighteen permanent plots were established in each forest, in 1995 for the wet forest and in 1997 for the dry forest. Plots had 150 m^2 surface and were fenced to prevent harvesting and trampling. Sporocarps (fungi fruiting bodies) were sampled on a weekly basis during the main fruiting period (September to December) until

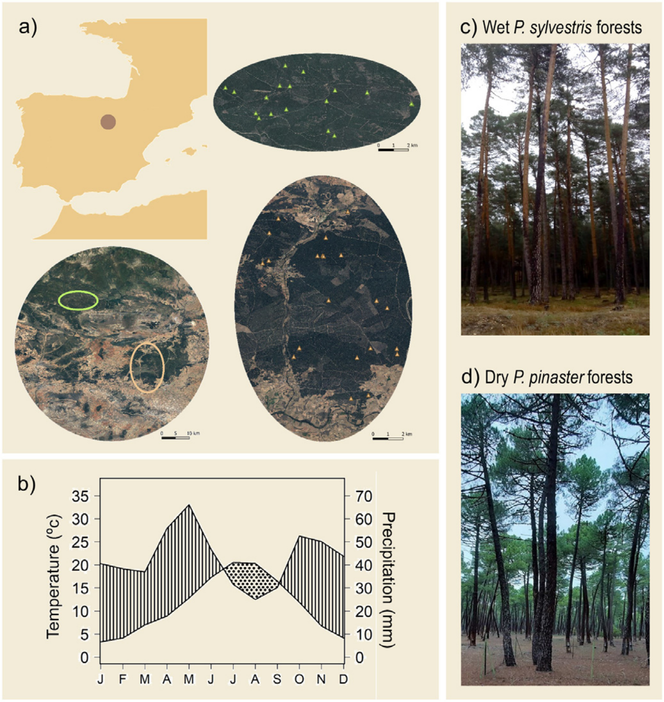

Fig. 1. Geographical location of study area and sampling plot design (a), climatogram of Soria city (b) and images of dry (*Pinus pinaster*) and wet (*Pinus sylvestris*) forests (c-d).

2018. All sporocarps within the plots were collected, fresh-weighed, identified to the species level and classified according to fungal guild (see Ágreda et al., 2015 for details). Dry forest plots were selected using a stratified design to represent all forest structures, whereas wet forest plots were located in bottom areas, thus increasing the difference in water availability among forest types.

For each forest, we obtained time series of annual mushroom yield. We also obtained annual time series of each of the main trophic guilds (saprophytic and mycorrhizal) as well as production of the main commercial species per site, i.e., saffron milk cap (*Lactarius deliciosus*) for the dry forest and king bolete (*Boletus edulis*) for the wet forest.

2.2. Climate and remote sensing data

Records of monthly temperature and total monthly precipitation were obtained from the Soria meteorological station (41°46′ 30″ N, 02°28′ 59″ W; 1082 m a.s.l., ≈35 km away from sampling sites, AEMET, Spanish Government) for the 1995–2018 period. Annual mean temperature was 11.1 °C, the coldest month being January (with mean daily minimum temperature of −1.2 °C) and the warmest month being July (with mean daily maximum temperature of 28.6 °C). Average annual rainfall was 517 mm, with a summer drought period typically occurring from mid-July to August (Fig. S1).

Soil moisture data were obtained from the ESA CCI combined Soil Moisture dataset with a spatial resolution of 0.25 × 0.25° (Dorigo et al., 2017; Gruber et al., 2017, 2019). These data are produced by merging both passive and active soil moisture datasets (Liu et al., 2012) and were available from 11/1978 to 12/2018 on a global scale. These include ASCAT scatterometer-based soil moisture data (ERS 1/2 and MetOp A/B satellites) and radiometer-based soil moisture data (SMMR, SSM/I, TMI, AMSR-E, WindSat, AMSR2, and SMOS). The merging between active and passive soil moisture products is done based on a weighted average method with the weights being proportional to Signal to Noise Ratio, estimated using triple collocation analysis of each product (Dorigo et al., 2013; Gruber et al., 2017). All these different datasets are scaled to a common model of soil moisture climatology, provided by the Global Land Data Assimilation System (GLDAS) Noah Land Surface Model (Rodell et al., 2004). More details about the theoretical and algorithmic base of this product and detailed analysis about the uncertainties of the soil moisture datasets can be found in Dorigo et al. (2017), Gruber et al. (2019, 2017) and Liu et al. (2012). Information about the daily CCI volumetric (m^3/m^3) soil moisture product can be retrieved at http://www.esa-soilmoisture-cci.org. For our study, monthly values of soil moisture were calculated as the average of available daily values.

We used the difference between summer NDVI and winter NDVI as an estimate of yearly primary productivity, since we considered this was the period that better explains tree performance in Mediterranean continental climates (Arzac et al., 2018b). NDVI data were extracted from LS-5, LS-7, and LS-8 NASA missions. NDVI values for all the 30-m side pixels that included each of the plots were obtained for every winter and summer season from the study period. We chose February 14th for winter and August 15th for summer. Since images for selected data were sometimes not available due to clouds interference, we searched for the closest date with a clear image available. We averaged NDVI values over the 18 plots per forest type, year and season.

2.3. Statistical analyses

2.3.1. Model parameters selection

As a first step, we selected climatic and remote sensing variables to be included in the definition of predictive models. To do this, we obtained Pearson's correlations between mushroom yields and monthly climate parameters (precipitation and minimum temperature) from June to December, according to the mushroom fruiting season. For each climatic parameter, we selected the month and the accumulated period with the highest correlation to be included in predictive models. This resulted in four climate parameters (two for precipitation, two for minimum temperature) per mushroom series (i.e., mushroom yields in wet forests, in dry forests, and production of the two main commercial species).

We followed the same procedure for selecting parameters about soil moisture data. Then, we obtained Pearson's correlations between mushroom series and NDVI data for the fruiting year. Since previous years' primary productivity may have a delayed positive effect on mushroom yields through the accumulation of photo-assimilates and/or organic matter that can be later used by fungi, we also correlated mushroom series with NDVI data from the previous year and from two years before (i.e., one and two-years lag). From these three temporal lags, we selected the one with the highest correlation to be included in predictive models. Since NDVI and primary productivity have a non-linear relationship, we also included a quadratic term of NDVI in the models (Wang et al. 2004b).

2.3.2. Model definition

We used the selected parameters to fit three different sets of linear models for each mushroom time series: (i) *Climate models*, using the four climate parameters previously selected, (ii) *Remote sensing models*, using two parameters for soil moisture and the best NDVI lag and its quadratic term, and (iii) *Combined models*, using climate and remote sensing parameters. Residuals of full models were analysed for normality using Shapiro-Wilk Normality test, if residuals for any of the three models of a times series were not normal, time series was square root-transformed for all three models to make results comparable. Residuals normality was achieved in all cases after transformation. For each set of models, we compared all additive combinations of explanatory variables using *dredge()* function from *MuMin* package (Barton, 2009) in R environment (R Core Team, 2019) and selected the most informative model following the Bayesian information criterion (BIC), which yields more conservative models than the Akaike information criterion (Aho et al., 2014). Variance Inflation Factors (VIF) were checked for the most informative models to search for multicollinearity. Since remote sensing data were not available for some periods, model comparison for remote sensing and combined models was based on a reduced dataset including solely years with complete datasets. Selected models were readjusted using all years available, thus penalizing estimated models.

2.3.3. Trophic guilds response to NDVI

Since fungi belonging to different trophic guilds show different feeding strategies, we assessed whether the main fungal trophic guilds showed distinct responses to primary productivity. In order to do this, we correlated mycorrhizal and saprophytic yields in both forest types with NDVI values at the fruiting year and with one and two-years lag.

3. Results

3.1. Mushroom yields data

We collected 1325 kg of mushrooms: 519.1 kg in dry forests (from which 71.4 kg were saffron milk cap, 13.8%) and 806.3 kg in wet forests (from which 182.5 kg were king bolete, 23.3%). Mycorrhizal fungi dominated both communities, with saprophytic comprising around 10% of the total fresh weight. Production per ha ranged from 87.3 kg in dry forests to 124.4 kg in wet forests, but with high interannual variability: coefficient of variation was 93.8% for wet and 81.7% for dry forests, being even larger for individual species (141.7% for milk saffron cap; 92.8% for king bolete). The relative contribution of these two species to the total yields also showed extreme variability, ranging from 0% to 23% for milk saffron cap and to 57% for king bolete.

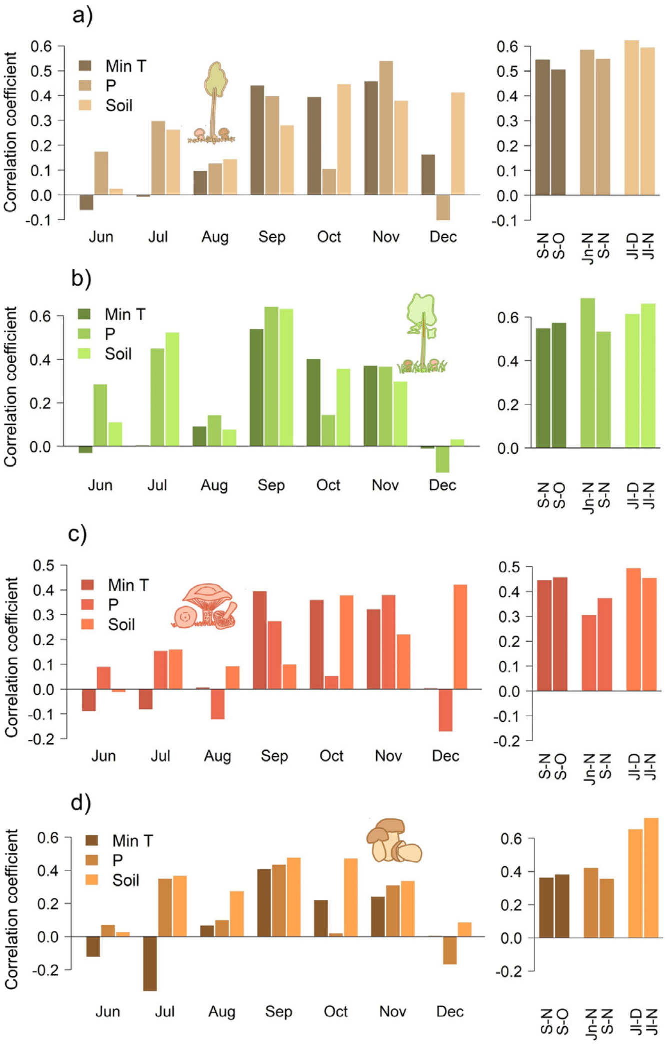

Fig. 2. Correlation between yearly mushroom biomass and minimum temperature (Min T), precipitation (P) and soil moisture (Soil) at monthly (left) and aggregated (right) periods for dry (a) and wet (b) pine forests, as well as for milk saffron cap *Lactarius deliciosus* (c) and king bolete *Boletus edulis* (d).

3.2. Selected predictors

3.2.1. Climate parameters

The best climate predictors (Fig. 2) for mushroom yields in dry forests ($n = 22$) were November ($r = 0.53$, $P = 0.011$) and summer-autumn (June to November) accumulated precipitation ($r = 0.59$, $P = 0.004$), as well as November ($r = 0.46$, $P = 0.032$) and autumn (September to November) ($r = 0.55$, $P = 0.009$) average minimum temperature. Climate predictors in wet forests ($n = 24$) peaked a bit earlier, in September ($r = 0.64$, $P < 0.001$) and summer-autumn (June to November; $r = 0.69$, $P < 0.001$) for precipitation, and in September ($r = 0.54$, $P = 0.007$) and early autumn (September to October; $r = 0.57$, $P = 0.003$) for average minimum temperature. Saffron milk cap showed marginally significant responses to November ($r = 0.38$, $P = 0.082$) and September to November precipitation ($r = 0.37$, $P = 0.088$), whereas its response to minimum temperature was marginal in September ($r = 0.39$, $P = 0.069$) and significant in September-October ($r = 0.46$, $P = 0.033$). The best predictors for king bolete production occurred in the same months as in wet forests, i.e., September ($r = 0.41$, $P = 0.034$) and June to November precipitation ($r = 0.42$, $P = 0.040$), and September ($r = 0.41$, $P = 0.049$) and September to October minimum temperatures ($r = 0.38$, $P = 0.067$).

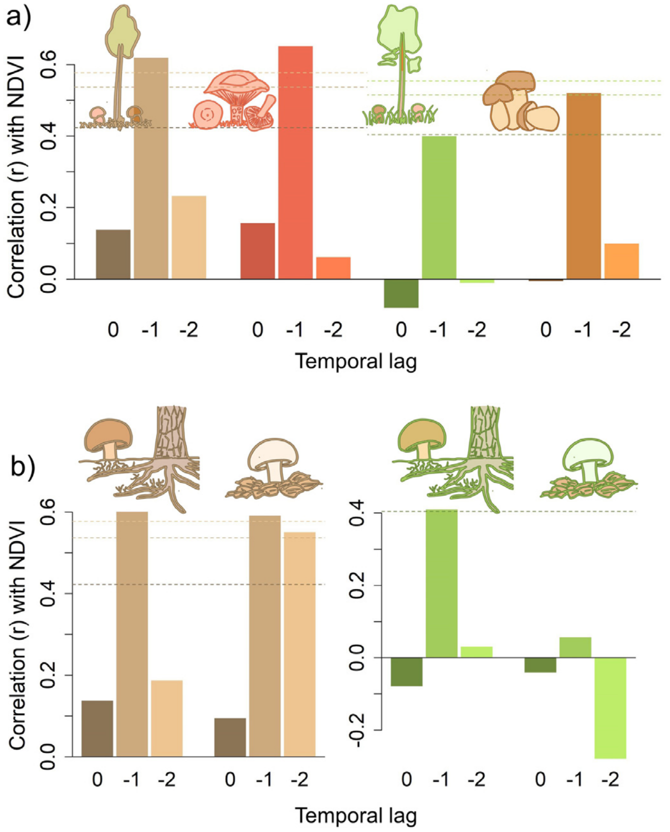

Fig. 3. Correlation between mushroom yields and NDVI (Normalized Difference Vegetation Index) in the fruiting year (lag = 0) and one and two years before (lag = –1 and –2, respectively). a) Correlation coefficients for each forest type and for the two main commercial species. From left to right: dry forests, saffron milk cap, wet forests and king bolete. b) Correlation coefficients for mycorrhizal and saprophytic guilds in dry forests (left plot) and in wet forests (right plot). Lighter bar colors are used for increasing temporal lags. NDVI increment was obtained as the difference of summer minus winter NDVI. Dashed lines with decreasing width indicate P values of 0.05 (the thickest), 0.01 and 0.001 (the thinnest).

3.2.2. Soil moisture data

Soil moisture in summer-autumn was highly correlated with mushroom yields, both in dry (July to December; $r = 0.63$, $P = 0.002$, $n = 18$) and wet (July to November; $r = 0.66$, $P = 0.001$, $n = 20$) forests (Fig. 2). The best monthly correlation occurred later in dry forests (October; $r = 0.45$, $P = 0.063$, $n = 18$) than in wet forests (September; $r = 0.63$, $P = 0.001$, $n = 23$). Saffron milk cap shared its accumulated signal period (July-December) with dry forests ($r = 0.49$, $P = 0.037$, $n = 18$), but the highest single-month signal occurred in December ($r = 0.48$, $P = 0.082$, $n = 18$), instead of October. King bolete shared the soil moisture signal with wet forests, peaking from July to November ($r = 0.72$, $P < 0.001$, $n = 20$) and in September ($r = 0.48$, $P = 0.019$, $n = 20$).

3.2.3. NDVI effect on yields

Both forest types and single species responded positively to NDVI in the previous year (Fig. 3a), although this response was marginal in wet forests ($r = 0.40$, $P = 0.053$, $n = 24$). Mushroom yields were neither significantly related to NDVI in the fruiting year, nor two years before, suggesting that fungal production depends on primary productivity in the previous year, instead of in the fruiting year.

Mycorrhizal mushroom production increased with higher NDVI increment in the previous year in both forest types ($r = 0.601$, $P = 0.003$, $n = 22$ for dry forests; $r = 0.410$, $P = 0.047$, $n = 24$ for wet forests), but did not respond to NDVI increment in the current year, or two years

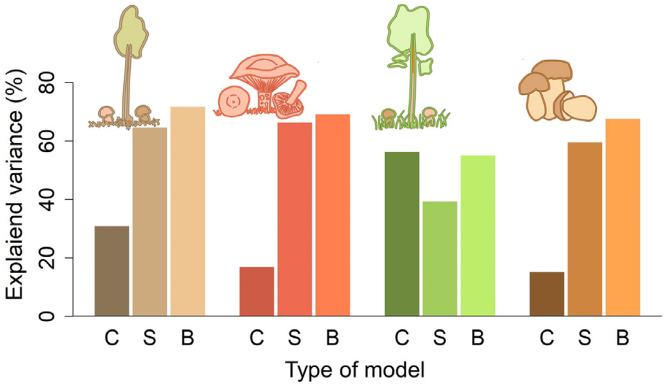

Fig. 4. Percentage of adjusted variance explained by climate (C), remote sensing (S) and combined (B) models. Selection of the most informative model was based on BIC. From left to right, results for mushroom yields in dry forests, milk saffron cap production, mushroom yields in wet forests and king bolete production.

before (Fig. 3b). Saprophytic mushrooms showed disparate results depending on the forest type. In dry forests, the saprophytic guild showed strong correlation with primary productivity at one- and two-year lags ($r = 0.60$, $P = 0.004$, $n = 22$ for one-year lag; $r = 0.55$, $P = 0.008$, $n = 22$ for two-year lag) and, in fact, a linear model including NDVI increments with one and two-year lags explained a large fraction of the variance ($R^2_{adj} = 0.536$, $P < 0.001$, $n = 22$). In contrast, we observed no relationship with NDVI increments at any lag for saprophytic mushrooms in wet forests (Fig. 3b).

3.3. *Models*

3.3.1. *Climate models*

Models for dry forests and single species were root transformed. Accumulated precipitation from June to November (Fig. 4, Table 1) was the only parameter included in the most informative model for explaining mushroom yields in dry forests ($R^2_{adj} = 0.399$, $P = 0.001$, $n = 22$). In wet forests, maximum yields occurred when wet June-to-November periods were combined with humid Septembers ($R^2_{adj} = 0.563$, $P < 0.001$, $n = 24$; Table 1). The most informative model for saffron milk cap yields only included accumulated September-October precipitation ($R^2_{adj} = 0.122$, $P = 0.063$, $n = 22$), whereas king bolete yields were higher in years with humid Septembers ($R^2_{adj} = 0.220$, $P = 0.012$, $n = 24$).

3.3.2. *Remote sensing models*

Average soil moisture from June to December and previous year and NDVI variation (Fig. 4, Table S1) explained a large part of mushroom yields in dry forests ($R^2_{adj} = 0.547$, $P = 0.001$, $n = 18$). In wet forests, previous year NDVI and soil moisture in September built the most informative model ($R^2_{adj} = 0.393$, $P = 0.003$, $n = 22$). Saffron milk cap yields responded to previous year July to December mean soil moisture and NDVI ($R^2_{adj} = 0.551$, $P = 0.001$, $n = 18$), whereas king bolete yields were maximal when high soil moisture from July to November occurred after a year with high NDVI ($R^2_{adj} = 0.750$, $P < 0.001$, $n = 20$).

3.3.3. *Combined models*

Mushroom yields in dry forests (Fig. 4, Table 1) increased when rainy conditions from June to November occurred after a previous year with high NDVI variation ($R^2_{adj} = 0.682$, $P < 0.001$, $n = 22$). Conditions for high mushroom yields were very similar in wet forests, with a positive effect of NDVI, June to November precipitation and high minimum September-October temperatures ($R^2_{adj} = 0.550$, $P < 0.001$, $n = 24$). The effect of NDVI increment in the previous year was significant for saffron milk cap and king bolete. The most informative model for saffron milk cap included accumulated precipitation from September to October and NDVI ($R^2_{adj} = 0.484$, $P < 0.001$, $n = 22$), whereas the model for king bolete included NDVI as well as the effects of high soil moisture from July to September ($R^2_{adj} = 0.750$, $P < 0.001$, $n = 20$). VIF < 2 in all cases, indicating no multicollinearity.

3.3.4. *Combined models provide better adjustment*

Combined models included more parameters and explained a higher proportion of variance than climate and remote sensing models on their own (Fig. 4, Table 1). Globally, combined models provided the best fit to the data (mean $R^2_{adj} = 0.629$), followed by remote sensing models (mean $R^2_{adj} = 0.561$). Climate models provided the worst fit (mean $R^2_{adj} = 0.326$) with the only exception of wet forests, for which climate models had the best fit (Fig. 4). Note that in remote sensing and combined models, the most informative model was selected excluding years with missing data on soil moisture and then R^2_{adj} was recalculated using all available data for the selected parameters, which yielded lower R^2_{adj} values.

4. Discussion

According to our first hypothesis, previous year primary productivity (inferred from NDVI) had a positive correlation with fungal yield. When exploring this signal at guild level, we found differences across forests: the signal was similar for mycorrhizal fungi in dry and wet forests, but differed for the saprotrophic guild. The effect was strong at one and two-year lags in dry forests, but disappeared in more productive wet forests. Data also supported our second hypothesis, since soil moisture inferred from RADAR sensors rivaled the predictive power of precipitation data. Finally, models including remote sensing and climate data improved models based solely on climate data, thus confirming our third hypothesis.

Soil moisture data based on remote sensors provided similar results than precipitation in predicting mushroom yields. Soil moisture values can be partially attributed to rain, but other parameters like temperature, insolation as well as other soil variables have also strong influence on daily and seasonal variations in soil moisture (Robock, 2014). In fact, long-term predictions for mushroom yields differ when evapotranspiration, instead of precipitation, is included in the models (Collado et al., 2019). Considering soil moisture values instead of climate parameters in predictive models therefore circumvents this limitation. Moreover, soil moisture along the fruiting season was linked with mushroom yields in a more stable way than precipitation, which suggests that the biological process was reflected in a more realistic fashion.

Considering the predictive power of NDVI as a surrogate of forest primary productivity also showed promising results. Growth of forest fungal mycelia is supported by trees either directly –through photo-assimilates transference (mycorrhizal fungi)– or indirectly –through the effect of higher biomass production on substrate availability for decomposers (saprophytic fungi)–. Different attempts have tried to link temporal series of tree growth with fungal production (Collado et al., 2019; Primicia et al., 2016) due to the existing relationship between tree growth and photo-assimilate levels (von Arx et al., 2017). Tree growth has shown promising results in Mediterranean pine forests, but this relationship might respond to common climatic control on tree growth and fungal production (Ágreda et al., 2015; Arzac et al., 2018a). In this sense, remote sensing NDVI data have the potential to link primary productivity with fungal growth, since NDVI is a more robust estimate of primary productivity than ring width (Schloss et al., 1999). But in addition, the consistent correlation we found between previous year NDVI and mushroom yields in all models that combined remote sensing with climatic data suggested a clear time domain separation between primary productivity and mushroom production, thus reducing potentially confounding effects due to a common climate forcing

Table 1
Parameters (Par) included in the most informative models explaining mushroom yields in (a) dry forests and (b) wet forests, as well as for the species (c) *Lactarius deliciosus* and (d) *Boletus edulis*. Climatic parameters include precipitation (P) and minimum temperature (T_{min}). Remote sensing parameters include soil moisture (soil) and the Normalized Difference Vegetation Index (NDVI), obtained as the difference of summer minus winter NDVI in the previous year (prev). Colored cells indicate that the corresponding predictor variable (in rows) was included for that month (in columns) or period (several consecutive months) in the most informative model. Dark blue in September in wet forests indicates the additive effect of September precipitation and the accumulated precipitation from June to November. All factors had positive effects on mushroom yield.

		a) Dry forests								b) Wet forests							
Model	**Par**	**prev**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**prev**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Climate	P		🟦	🟦	🟦	🟦	🟦	🟦			🟦	🟦	🟦	■	🟦	🟦	
	T_{min}																
Remote sensing	soil			🟫	🟫	🟫	🟫	🟫	🟫					🟫			
	NDVI	🟩								🟩							
Combined	P		🟦	🟦	🟦	🟦	🟦	🟦			🟦	🟦	🟦	🟦	🟦	🟦	
	T_{min}													🟨	🟨		
	soil																
	NDVI	🟩								🟩							

		c) *Lactarius deliciosus*								d) *Boletus edulis*							
Model	**Par**	**prev**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**prev**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Climate	P					🟦	🟦	🟦						🟦			
	T_{min}																
Remote sensing	soil			🟫	🟫	🟫	🟫	🟫	🟫			🟫	🟫	🟫	🟫	🟫	
	NDVI	🟩								🟩							
Combined	P					🟦	🟦	🟦									
	T_{min}																
	soil											🟫	🟫	🟫	🟫	🟫	
	NDVI	🟩								🟩							

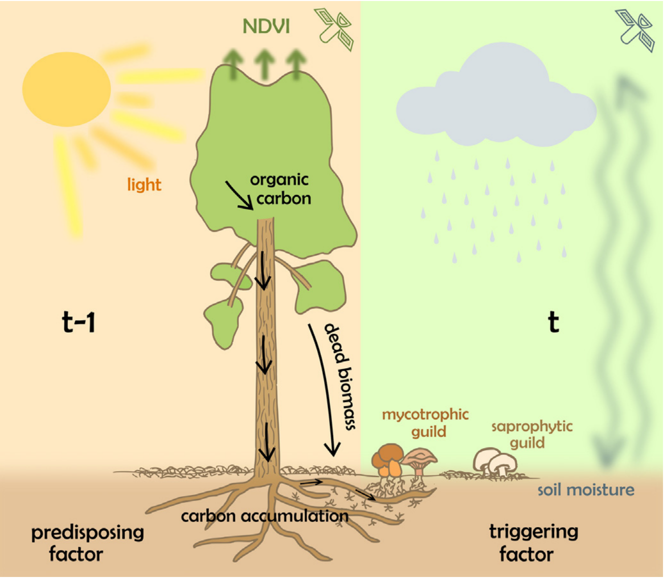

Fig. 5. Schematic view of the working hypothesis proposed to study environmental factors that control mushroom production. Primary productivity (NDVI) in a given year (*t*-1) controls carbon gain, leading to carbon accumulation in roots. Higher carbon accumulation would favor the development of mycorrhizal fungi, enhancing mushroom yields of mycorrhizal species in the following year (*t*) and thus acting as a predisposing factor. In the case of saprophytic fungi, the accumulation of dead biomass under tree canopies would also promote mushroom production in the following year or even two years later. In any case, final mushroom production would depend on the existence of favorable weather conditions (humidity, temperature…) during the fruiting season (triggering factor).

(Collado et al., 2019).

Our study suggests that trees' resource accumulation in a given year might promote fungal production in the next fruiting season. Since different fungal guilds use different resources, contrasting responses were expected between saprophytic and mycorrhizal fungi and, in fact, we found some support for this expectation. Mycorrhizal fungi were correlated to primary production in the previous year. Since mycorrhizal fungal biomass depends on carbon transfer by the host (Allen, 1991), this correlation with NDVI in the previous year might be attributed to a direct benefit from higher tree resource availability. The effect on saprophytic fungi, on the contrary, was indirect and depended on site productivity. Saprophytic fungi in less productive dry forests showed strong positive responses to primary productivity with one and two-year lags. In this managed forest with low availability of dead wood, litterfall provides the main substrata for saprophytic fungi. Higher primary productivity has been shown to have a direct effect on litterfall (Schlesinger 1997; Wang et al., 2004b), albeit with some lag for perennial species. Thus, in our pine forest, it could be expected a one to two years lagged effect of primary productivity on litterfall, posing a plausible explanation for the lagged correlation between NDVI and saprophytic fungal development. In contrast, the saprophytic fraction from more productive wet forests did not respond to primary productivity at any temporal scale, probably due to the existence of higher biomass accumulation, but also to the topography of sampling plots, which were located in bottom areas, being subsidized with organic matter from surrounding areas. With plenty of organic matter, mushroom production control would only depend on weather conditions at annual scale.

Based on these results, we propose as working hypothesis that mushroom production may respond to a two-step process: resource accumulation during the previous year would determine the energy available to support mycelial growth, acting as a predisposing factor, whereas weather conditions during the fruiting season would regulate the ability of mycelia to transform this energy into fruiting bodies, acting as a triggering factor (Fig. 5). This hypothesis might help to understand how environment control mushroom production, but we are aware that our current results only suggest limited evidence to support it. Therefore, future studies should test and validate (or falsify) this hypothesis with experimental work along forests with different productivity and fungal communities.

5. Conclusions

The combination of remote sensing sources with climatic data improved our ability to model mushroom production in two Mediterranean pine forests with contrasting humidity levels. Our soil moisture dataset was based on coarse-grained data, but novel remote sensing products for soil moisture already allow the estimation of soil humidity at higher spatial (decameters) and temporal (days) resolution (ESA – Copernicus, 2014). Moreover, fine-grained daily temperature values are also available with remote sensing methods in a daily fashion (Wang et al., 2004a), and remote sensing data on primary productivity are at a very mature stage, multiple satellite-based data being freely available. Altogether, our results open a path to use remote sensing data at high spatio-temporal resolution to face the challenge of predicting intra-seasonal mushroom yields over space and time.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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