

Impact of local and regional climate variability on fungi production from *Pinus sylvestris* forests in Soria, Spain

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Abstract

The cultivation of edible fungal species represents a profitable agricultural sector and an interesting climatic-impact oriented topic. This article focuses on *Boletus edulis* that develops in *Pinus sylvestris* forests in Soria (Castile and León in the Iberian Peninsula). This work aims at evaluating the extent to which the climate variability modulates the fungi production, both at local and regional/synoptic scales. With this purpose, the relationship between *B. edulis* production and various climatic variables such as precipitation, temperature, soil moisture and soil temperature has been explored based on observations during 1995–2014 over the study area as well as reanalysis data. The study evidences the relative importance of humidity in the *B. edulis* production both at the surface and the subsurface. In general, it can be said that wet conditions early in the production season together with cooler summers and mild autumns enhance the *B. edulis* growth. Evidences of the particular relevance of soil conditions at the beginning of the production season on the total annual production have been provided. In addition, the age of the trees that host the fungi species seems to play as well a pivotal role in the amounts of production obtained. Such a detailed analysis, including local relevant climatic information along with the investigation of the large-scale features that impact the production of edible fungi species has not yet been developed over this region.

KEYWORDS

Boletus edulis production, climate variability, edaphoclimatic conditions, Iberian Peninsula, large-scale circulation, tree age

1 | INTRODUCTION

Climate variability has a significant influence in human ecosystems, especially in the agricultural sector. In general, the croplands and farmlands all around the globe are largely affected by climate variations at all timescales. In particular, response of ecosystems to climate variability has been documented for a vast variety of fungal species (Martínez-Peña *et al.*, 2012b; Büntgen *et al.*, 2013;

Boddy *et al.*, 2014). It has been reported that year-to-year variations and long-term trends in the appearance and development of fungi products, as well as drifts in the timing of harvests, could be associated with land-use/land-cover changes and climatic fluctuations (Büntgen *et al.*, 2015).

Knowledge about how climatic conditions may influence the fungi emergence and growth is hampered by the lack of complete and continuous observed production

records, with usual unsatisfactory length and/or resolution of measurements (Büntgen *et al.*, 2012). Understanding variations in mycological products yields as well as their connection to climate is of most relevance not only from an environmental and scientific perspective but also from an economic standpoint, provided that some of the edible fungal products are worldwide considered precious and expensive exquisiteness (Hall *et al.*, 2003).

Ectomycorrhizal fungi taxa remain mostly in the microbial stage below the surface. They develop an intricate network of mutual benefits with the root structure of their host plants and trees: mycorrhizas can enlarge the area of nutrients absorption of their hosts, specially phosphorus. Correspondingly, the host tree grants the fungal bodies the availability of carbohydrates and a suitable environment that nourishes the bodies and favours their proliferation. This study focuses on *Boletus edulis*, a fungi symbiotically associated with the tree species *P. sylvestris* (Martínez-Peña *et al.*, 2004). They grow in a broad range of habitats throughout the Northern Hemisphere and were haphazardly introduced into New Zealand and - South Africa. *B. edulis* is an appreciated ectomycorrhizal fungus species consumed all over the world. The fruiting bodies have a very strong flavour and are widely used both commercially and domestically, particularly frequent in temperate forests of North America and Europe (Hall *et al.*, 1998; Boa, 2004). This variety can be found in a symbiotic network with a considerable diversity of trees and scrubs and is usually found in *P. sylvestris* forests of the Iberian Peninsula (Águeda *et al.*, 2008), where large amounts of these fungal bodies are produced (more than 40 kg of sporocarps/ha-year on average; Martínez Peña *et al.*, 2009). The sporocarp growth has been associated with climatic influences and phenology (Gange *et al.*, 2007; Kauserud *et al.*, 2008, 2010; Büntgen *et al.*, 2012). Additionally, the fungus production is connected to the stands structure and site particularities (Martínez-Peña *et al.*, 2012b; Taye *et al.*, 2016). The land plot basal area (Martínez-Peña *et al.*, 2012b), the age category (Martínez-Peña *et al.*, 2012a) and air temperature (Hernández-Rodríguez *et al.*, 2015) have been identified as relevant forcing factors of the *B. edulis* sporocarps over the northern Iberian Peninsula.

In the Northern Hemisphere, some of the most important *P. sylvestris* forests are located in the Mediterranean area. It should be however noticed that the expansion of these forests, even if they occupy large areas, is moderate if compared to forests of the same species in central and northern Europe. The growth of *P. sylvestris* forests is inhibited by water deprivation during droughts as well as the very high temperatures in the warm season. Summer drought has been identified as the dominant stress agent in limiting the development and healthy

spread of plant and tree species over most of the Mediterranean regions (Sabaté *et al.*, 2002). Current annual potential evapo-transpiration is larger than the amount of precipitation received over these regions throughout the year, although precipitation presents high intra- and inter-annual variability (Hartmann *et al.*, 2013).

In the Iberian Peninsula, the *P. sylvestris* is autochthonous in the three largest mountain ranges, Pirenees, Iberian System and Central System. Our region of interest, Pinares, is located within the Iberian System in the province of Soria in Castile and León (see Figure 1). Fungi harvest has an important economy impact in the region. This activity contributes to the livelihood economies and also represents a relevant financial support in rural regions. In addition, edible fungi species are also the basis of several craft products, including medicinal products. Mushrooms are as well the engine of a new branch of eco-tourism with its basis on programmes associated to nature (Egli *et al.*, 2006; Martínez-Peña *et al.*, 2012a; Díez *et al.*, 2013). Approximately a 35% of the rural population in Castile and León is devoted to fungi harvesting either with commercial or self-supply purposes.¹ Years with generous yields, more than 15.000 tons of mushrooms can be marketed.

It is, therefore, of great importance to establish which factors are influencing fruit-body emergence and development. The vast majority of fungal species live in symbiosis with their host trees, therefore, the soil composition and in general, the stand characteristics, that are usually modified according to the forest management plans, may impact edible mycorrhizal species production. More than this, the inter-annual variability of mycological production is hypothesized to be highly influenced by climate conditions like precipitation, temperature, soil moisture and soil temperature (Martínez-Peña *et al.*, 2012a).

Phenological changes are among the most sensitive ecological responses to climate variations (Buentgen *et al.*, 2012). Edible fungi species growth and production have proved affected by recent climate trends and change. Recent studies report extension of the fungi-growing season over Europe in general and over the Mediterranean region in particular, due to an earlier onset of fungi sprouting plus a delay of the season termination, due to warmer conditions during November and December, whose temperatures usually determine the offset of the production period. The later has also been connected to increased temperatures and precipitation rates in August and October on average, respectively (Kauserud *et al.*, 2008; Karavani *et al.*, 2018). Nonetheless, a severe reduction of the emergence and productivity of diverse fungal taxa, in particular symbiots, in various parts of Europe has also been related to pollution and climate change influences (Ágreda *et al.*, 2015).

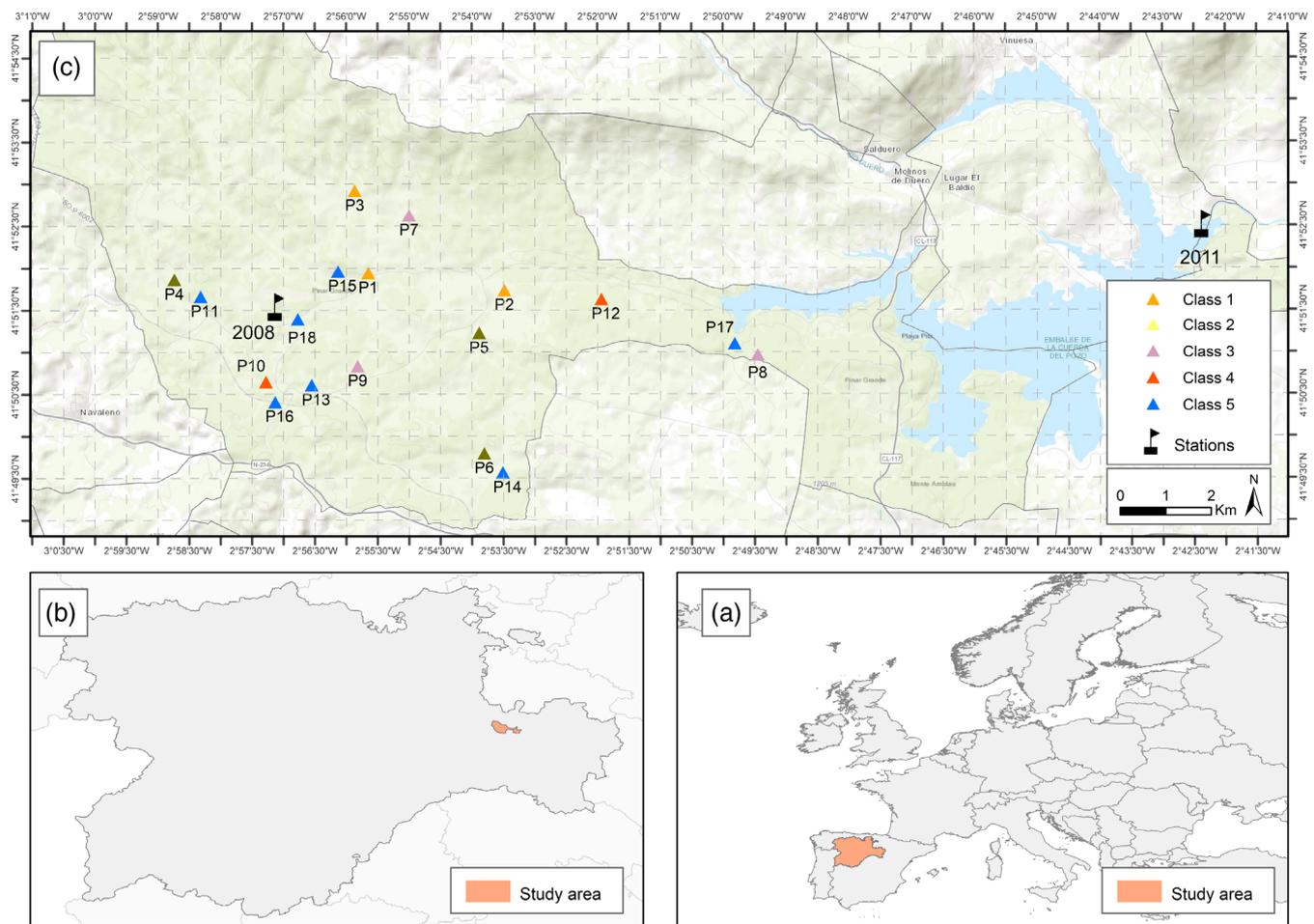


FIGURE 1 (a) Study area in north Central Iberian Peninsula. (a) Region of Castile and León (orange) where the province of Soria is located; (b) Zoom-in over Soria, the *Pinar Grande* area, where the land plots are placed, is highlighted in orange; (c) Zoom-in image of the land plots location. Each triangle represents a land plot. They appear segregated in colours according to their corresponding tree age-class. See text for further details [Colour figure can be viewed at wileyonlinelibrary.com]

Many of the most well-known edible varieties, such as those belonging to the group of *B. edulis*, pertain to this category (Salerni and Perini, 2004).

Over our region of interest, influences of climatic factors have been investigated on the ectomycorrhizal mushroom (*B. edulis* and *Lactarius deliciosus*) production (Sabaté *et al.*, 2002; Büntgen *et al.*, 2015). Notwithstanding, dominant climatic driving factors are still not sufficiently clear. There are hints of mean September, October and November temperatures being the most influential factors in this fungal species growth and production (Martínez-Peña *et al.*, 2012b). In addition, other works identify precipitation as a pivotal factor in fruiting-bodies emergence and harvesting (Karavani *et al.*, 2018). Stand structure and properties (age, basal area, height or slope) have also been identified (De la Varga *et al.*, 2013) as relevant agents. Relatively less explored in this area is the role of soil conditions. Soil properties such as water retention capacity, soil texture and pH have proved

strong correlation with mushroom yield (Martínez-Peña *et al.*, 2012a). However, edaphoclimatic conditions (soil temperature and soil moist) have not yet been widely investigated in their relation to ectomycorrhizal mushrooms growth. A few attempts in the literature dealing with water balance processes to estimate soil moisture and its influence on the fungal fruiting can be found (Ágreda *et al.*, 2015; Karavani *et al.*, 2018).

Since it can be difficult to segregate the local climatic conditions that might affect fungal species from those non-climatic factors such as soil properties, stands structure, vegetation characteristics, and so forth, that typically have a sensible effect on fungi growth, an approach based on more regional—large scale circulation features may help the identification of robust climate influences, potentially unaffected by non-climatic elements. Only a few studies have identified the regional character of the climatic features influencing the fungi production in order to isolate synchronous responses to future climate

change at the continental scale (Büntgen *et al.*, 2012, 2013). Disentangling whether there are dominant large-scale patterns that lead the generation and growth of the fungal products might have relevant implications concerning for instance decision-making and management issues. It is also relevant for the understanding of the dynamics that enhance or hamper the *fungi* production, which in turn might ease estimations of seasonal or long-term future production. In addition, it may be of interest for modelling studies that simulate the atmospheric and soil conditions that favour mushroom production but do not deal with biological factors (e.g., regional climate models, Büntgen *et al.*, 2015). To our knowledge, the relation between fungi production and the relevant large-scale atmospheric patterns over our region of interest remains unexplored up to date.

The main objective of the present work is to illustrate the relationship between climate variability and *B. edulis* based on the collection of this edible fungal species reported throughout two decades over north central Iberian Peninsula. The aim of the article is three folded. On the one hand, we examine the influence of the local climatic conditions of *Boletus* growth by exploring the links between instrumental records of surface air temperature and precipitation from nearby meteorological stations and the fungi production. Additionally, the association between climate and *Boletus* generation is examined from a wider perspective that accounts for the influence of the large scale circulation on the *B. edulis* growth. Such an hypothesis assumes that the synoptic variability is a natural driver of the mushroom production over large regions in addition to the pivotal role of the local climate on the specific area of interest. These two objectives are based on approaches that search the linear associations between the fungal species and climate; therefore, we seek for variations of the climatic states that are followed by changes in the production. Finally, this work aims at highlighting the fundamental control of the edaphoclimatic conditions in triggering/hampering the *B. edulis* production. Thus, we explore the effectiveness of the soil temperature and soil moisture in activating the onset/termination of the production season. An analysis with these characteristics compiling local and regional climate variations and their possible associations to the edible fungal growth has not been extensively conducted over the region under study.

This article is organized as follows: Section 2 presents the *B. edulis* production data as well as the climatic variables used in the study; Section 3 describes the methodologies applied in the analyses while Section 4 describes and comments the results and finally, Section 5 features the main conclusions and emphasizes the need for further investigations.

2 | DATA

2.1 | *B. edulis* production variables

B. edulis production series spanning from 1995 to 2014 (20 years) have been used for this study. These series were collected in 18 stable plots located in unmixed even-aged stands of *P. sylvestris* forests, within the area of *Pinar Grande*, a large forest mass of 12.532 ha, in the Iberian System Mountains (Soria, Figure 1a). In *Pinar Grande*, the tree surface occupied by *P. sylvestris* constitutes 70% of the total tree mass.

Five classes are defined according to the age of *P. sylvestris* specimen, being class 1 the one with younger trees and class 5 the corresponding to the older ones (see Table 1 for class and age classification). Three land plots per class are considered, except in the case of class 5 with seven plots (due to its regeneration particularities, larger heterogeneity characterizes this age class group) and class 4 with only two plots. In Figure 1c, the 18 land plot sites are represented in different colours depending on the age-class.

Plots extension is 35 m × 5 m and they are fenced with 2 m tall hunting mesh, to avoid livestock, wild animals and pickers non-desired impacts. Every August the plots grass is mowed to ease the location of fungi bodies later during the production season. Our study is focused on the *B. edulis* species since this variety registered continuous weekly production every year during our monitoring period. Sampling was performed in the plots on a weekly basis from week 35 to 50 every year from 1995 to 2014. All fully developed sporocarps were collected and identified to species level in the laboratory. Number, fresh weight (g) and cap diameter (cm) of each *B. edulis* sporocarp collected was recorded. Due to the fact that sporocarps are collected every week, the specimens may have not reached their maximum size.

The production at each plot is denoted as p_x , with $x = 1, \dots, 18$. Fungi production can be expressed either in weight (g) or in number of fruiting bodies. The average number of bodies produced over all land plots is denoted as P_B . Additionally, P_W stands for the mean production in weight units. To take into account the fact that the age-class of the host trees might have an impact on the fungi amounts, we also define a *stratified mean production*, P_S , following Martinez-Peña (2008), as:

$$P_S = \sum W_i P_i \quad (1)$$

where P_i is the mean production per age class i (with $i = 1, \dots, 5$) calculated following:

TABLE 1 Stratification classes of the 18 land plots according to the host trees age (w.r.t. 1995), elevation and slope of each plot

Land plots	Age-class	Age (years w.r.t. 1995)	Elevation (m)	Slope (%)
1	1	<15	1,110–1,119	1
2	1	<15	1,110–1,119	4
3	1	<15	1,130–1,139	5
4	2	16–30	1,150–1,159	2
5	2	16–30	1,110–1,119	5
6	2	16–30	1,140–1,149	1
7	3	31–50	1,120–1,129	2
8	3	31–50	1,110–1,119	3
9	3	31–50	1,140–1,149	1
10	4	51–70	1,140–1,149	4
11	5	>70	1,140–1,149	1
12	4	51–70	1,110–1,119	4
13	5	>70	1,140–1,149	1
14	5	>70	1,140–1,149	1
15	5	>70	1,120–1,129	1
16	5	>70	1,150–1,159	4
17	5	>70	1,110–1,119	1
18	5	>70	1,120–1,129	2

$$P_i = \sum \frac{P_{class_i}}{n_i} \quad (2)$$

with p_{class_i} being the production in $g \cdot ha^{-1}$ of each land plot within age class i and n_i is the total number of land plots belonging to age class i . W_i in Formula 1 is the extension occupied by class i (see weights in Table S1 in the Supporting Information). Therefore, the stratified production is weighted according to the extension of the corresponding plot and it is measured in kilogram per hectare.

The variability of the *B. edulis* production throughout the monitoring period is shown in Section 4.1 where the connection between these data and the available meteorological records is also explored.

2.2 | Climate data

2.2.1 | Instrumental measurements

Local instrumental records are of two types: atmospheric and subsurface data. Atmospheric variables have been obtained from two meteorological sites: site n° 2008 (known as *El Amogable*) located at 1.150 m above ground level (a.g.l) and site n° 2011, both belonging to AEMET, the Spanish Met Office. Their location with respect to the plots is indicated with stars in Figure 1b.

The available observations at these sites are daily precipitation (mm) and temperature (mean, maximum and minimum, °C). Temperature data is available for site 2008 (2011) for the period 1994–2008 (1994–2014, with the year 2012 missing). Precipitation data is available also at both sites during the period 1994–2014, (data for 2012 is also missing at both sites). The missing gaps correspond to the change of the institution responsible of collecting the data. Both temperature and precipitation series at the two sites stations were subjected to a basic quality control procedure (such as the detection and deletion of unrealistic or out-of-physically-plausible-range values).

The soil climatic variables used in this analysis are the weekly mean, maximum and minimum soil temperature (SoilT_{mean}, SoilT_{max}, SoilT_{min}, respectively, in °C) and soil moisture (SoilM_{mean}, SoilM_{max}, SoilM_{min}, in $m^3 m^{-3}$) measured at each of the 18 land plots and averaged over all of them. Ground temperature sensors are installed at 20 cm depth at each plot. Volumetric soil content below-ground was measured using Decagon 5 TM probes (Decagon devices Inc.) at each plot. Soil sensors were placed in the middle of each plot, 15–20 cm below-ground, and measurements were recorded on a data logger EM50 (Decagon devices Inc.). Available measurements of soilT and soilM cover the period 2012–2014. Original data had weekly and daily frequency.

2.2.2 | Large scale data

The reanalysis allows for more robust correlation estimates since long time series with no missing data can be used. The large-scale information was provided by several variables from the ERA-Interim reanalysis (Dee *et al.*, 2011) This is a global atmospheric reanalysis that covers from 1979 up to present. The procedure to generate the reanalysis fields includes a four-dimensional variational analysis (4D-Var). The horizontal resolution is approximately 80 km (T255 spectral) with 60 atmospheric vertical levels from the surface reaching 0.1 hPa. There is a large variety of gridded 3-hourly reanalysis variables describing the atmospheric state as well as the ocean-wave and land-surface conditions, and 6-hourly upper-air parameters covering the troposphere and stratosphere. The ERA-Interim reanalysis variables used in this analysis are the temperature (2mT, °C), the mean sea level pressure (SLP, mbar), the volumetric soil water level 2 (soilM_{L2}, top soil layer at 14 cm, m³m⁻³), and total precipitation (Pre_{Tot}, mm). The geographical window covers 50° W–20° E and 30°–65° N.

3 | METHODOLOGY

The following paragraphs include a brief description of the approaches followed in this analysis to evaluate the relation between the climatic variations and the mushroom production in Pinar Grande at various spatial and temporal scales. The first two parts explore linear associations between climate and the mushroom growth: on the one hand, the linear link between the local climate and the *B. edulis* series is explored while the following part also analyses a linear connection between climate and the mushroom production but in this case focusing on the large scale circulation. Finally, the study proposes an approach to examine the non-linear influences of the edaphoclimatic fluctuations (soil temperature and moisture variability at the land plots level) on the *B. edulis*.

In order to evaluate a potential linear *Relation between the local climate and the B. edulis production* in Section 4.1, we investigate to what extent local climate fluctuations lead changes in the production. If linearity is detected it implies that if temperature or precipitation increases or decreases, the *B. edulis* production reacts thereupon. To this aim, simultaneous and lagged Pearson correlation coefficients between instrumental temperature and precipitation at the sites 2008 and 2011 and *B. edulis* production have been calculated. Note that all correlations are obtained between detrended anomalies with respect to their long term annual cycle (i.e., relative to the period 1995–2004). Simultaneous herein

implies that the correlation is calculated between climate and production reciprocal months. This is done in two different ways. First, the correlation is calculated separately for every production month from September to December (S, O, N and D) to analyse concurrent growth reactions to climatic influences (note that months names have been abbreviated herein). Additionally, the influence of the average climatology over the previous several months on the accumulated production of *B. edulis* for the same months is also explored. The latter is denoted as extended production season. Note that the accumulated *B. edulis* production values are obtained by adding the corresponding monthly production amounts: September + October (SO), September + October + November (SON) and September + October + November + December (SOND), while in the case of climate variables, this combination is obtained by averaging over the same months. These two estimations of co-linearity are denoted as simultaneous or lag = 0 correlations.

Furthermore, the lagged correlations up to 3 month lags that may account for the relative importance of the climate variations that took place before the onset of the production season in September on the amount of fungi collected has also been calculated. Thus, we calculate the correlation between the production in September with the average temperature over August and September (this is denoted as lag = 1, AS), also with the average over July, August and September (lag = 2, JAS), and finally with the average temperature of June, July, August and September (lag = 3, JJAS). The same way of calculating lagged correlations applies in the cases of the accumulated SO, SON, SOND production described in the previous paragraph.

The statistical significance of the correlation coefficients was calculated by applying a t-Student test. The test is aimed at identifying those correlations that are significantly different from zero. The critical values based on a T-Student two-sided distribution and the n-2° of freedom ($n = 20$ since we have 20 years of *B. edulis* production records) have been used to determine the threshold correlation (Eid *et al.*, 2017). Based on the previous we determine that all correlations equal or above/below ± 0.4 are significantly different from zero at a .05 level of significance ($p < .05$) or at a 95th confidence level and the null hypothesis (the variables are uncorrelated) is rejected for all correlations above this threshold.

Correlation maps allow an understanding of the synoptic patterns that influence the production of fungi over the northern Iberian Peninsula, enhancing a more regional perspective, complementary to the local view provided by correlation with instrumental measurements at the AEMET sites (see Figure 1). These maps are

presented in the Section 4.2. The correlation maps are obtained between the annual *B. edulis* production and the 2mT, Pre_{Tot} , SLP, and $SoilM_{L2}$ from the reanalysis fields using only the corresponding production month (October in the main text and also September and November that can be found in the Sup. Mat.), therefore, with lag = 0, but also considering the climatology over the previous months, thus with lags = 0, 1, 2, 3 months. Correlation values equal or above .4 are statistically significant for a 95th confidence level.

In order to examine whether the production of this fungus species can be related to some extent to the variability of the main modes of circulation over Europe and the Mediterranean region, the simultaneous correlation between individual months (September, October, November and December) of the production series and the North Atlantic Oscillation (NAO), the East Atlantic (EA), the Scandinavian (SCAND) and the East Atlantic/Western Russian (EAWR) patterns (Barnston and Livezey, 1987) has been calculated. Note that correlation values equal or above .4 are as well significant for a 95th confidence level.

The correlation provides some insight into the co-variability of production and climate variability. Thus, when one variable increases, the other does as well (or the opposite). However, many other local climatic and non-climatic factors (biological, geological, human-induced) are involved in the process of growth and maturation of the fungi bodies, therefore, non-linearity is to a great extent expected in these mechanisms. With the purpose of isolating potential relationships that do not lie within the range of linear associations, dispersion diagrams between production and measurements of soilM and soilT are investigated in Section 4.3. To this aim, weekly values of soilM and soilT are represented against the corresponding *B. edulis* production for each age-class average, allowing thus to explore plausible ranges of production depending on the soil conditions together with the influence of the age of the host pine trees. Finally, a selection of early and late *B. edulis* production may serve for the purpose of identifying the soil characteristics that are more related to the initiation/termination of the production season.

4 | RESULTS AND DISCUSSION

This section is devoted to show and discuss the potential relationships between the *B. edulis* production variations throughout the observational period and the climatic variability at different spatial scales. The three subsections aim at presenting an effective division of the spatial scales of interest.

4.1 | Relationship between local climate and *B. edulis* production

The following paragraphs illustrate the variations of the amounts of mushroom collected. The temperature and precipitation data recorded at the two meteorological stations described in Section 2.1 as well as the soil temperature and soil moisture over the 18 land plots are identically presented in this section. In this subsection, an insight about how the *B. edulis* production is conditioned by the local climate variations is also provided.

Figures 2–4 show the weekly production of *B. edulis* for the 20-year recorded time series from 1995 to 2014, only for the production season (SOND). According to the number of bodies (P_B in Figure 2a) the production is not homogeneous throughout the whole sampling period. The production during the first 10 years seems to be larger than during the second half of the period. However this is not so noticeable if P_W or P_S are observed instead (Figures 2b and 4a, respectively). The latter may indicate a relatively decrease of the number of bodies amounting nevertheless to a similar total weight during the most recent years. P_S in Figure 4a evidences the effect of the area weighting of plots with the same age (stratification). P_S shows large variability with years amounting for very little production and years peaking to large amount of *B. edulis* production, as for instance 1997–1998 and 2013–2014. Nevertheless, P_W and P_S share comparable variability as shown in Figures 2b and 4a (notice the change of scale). The relative contribution of each age-class to P_S can be observed in Figure 4b. The youngest ($p_{class\ 1}$ in green) and oldest ($p_{class\ 5}$ in blue) *Pinus sylvestris* specimens tend to produce smaller amount of fungi if compared to intermediate age-classes. The largest contribution to P_S is associated to age-class 4 (red in Figure 4b), therefore, for trees ranging from 50 to 70 years. Figures S1 and S2 show the p_{class_i} according to the age-class both for the number of bodies and production weight, respectively, together with the corresponding average (in black) over all 18 plots (P_B and P_W).

A question that seems pertinent is whether a relationship between the amount of fungi bodies and their weight can be identified. Figure 5 shows a dispersion diagram of the different p_{class_i} , where colour indicates the corresponding trees age-class. Two differentiated behaviours can be noticed in Figure 5. First, in the range of lower to medium weights the number of bodies is qualitatively comprised as well between low and medium, therefore, there is an apparent relation between both variables, weight and number. However, this does not necessarily holds for the larger amount of bodies, where the weight of fungi bodies is limited to the medium range. Thus, it can be said that a larger number of body counts

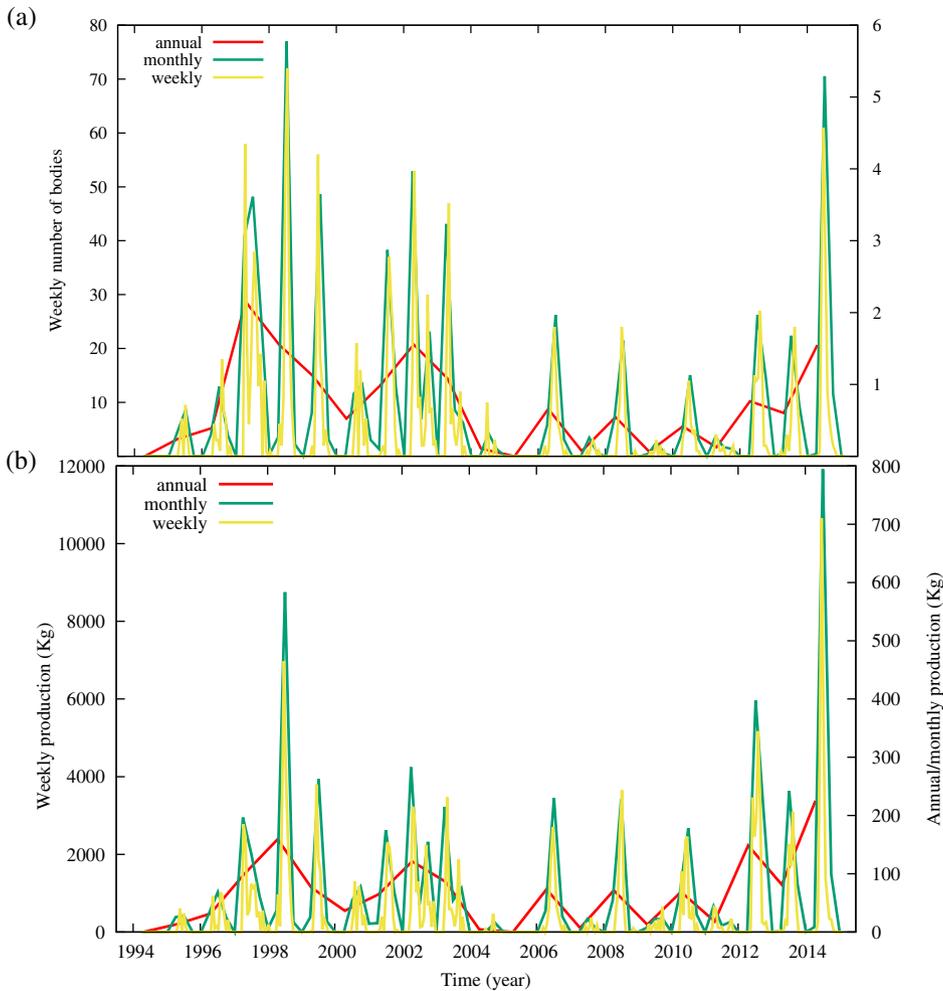


FIGURE 2 (a) Time series of mean *Boletus edulis* P_B (mean production in number of bodies) over the period 1995–2014 for the sampling season (September to December). In the left y axis the blue series corresponds de weekly mean production while in the right axis red stands for the annual averages and the green one represents the monthly means; (b) as in (a) but for P_W (mean production in grams) [Colour figure can be viewed at wileyonlinelibrary.com]

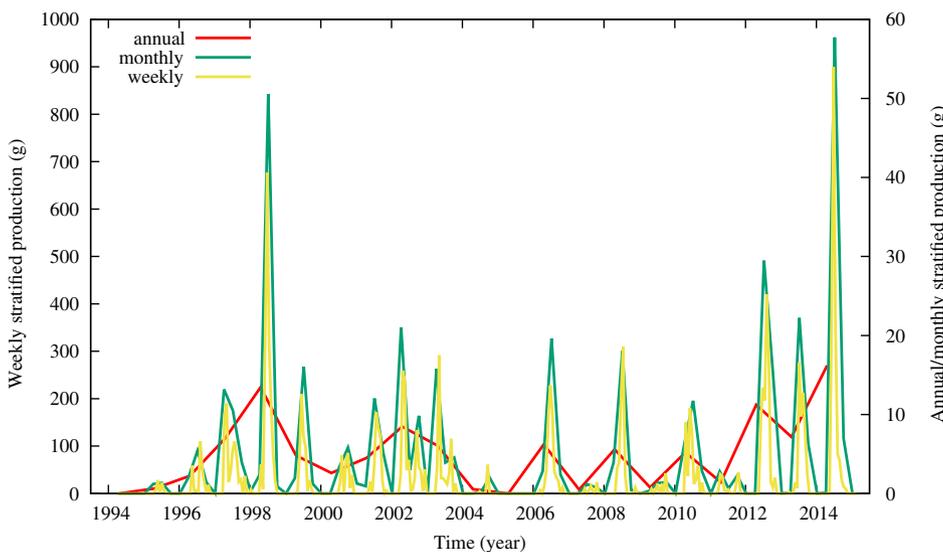


FIGURE 3 (a) As in Figure 2a but for P_S (stratified mean production also in grams) [Colour figure can be viewed at wileyonlinelibrary.com]

apparently limits the size of the fruit and thus, the larger P_B would not necessarily imply larger P_W , as already observed in Figure 2a,b.

In Figure 6, the weekly precipitation anomalies with respect to the long-term mean are shown. For the

monthly precipitation time series Figure S3 on the Supporting Information the correlation values between both sites calculated from January to December is $r = .62$, while if we consider only data for the production season (September to December), the correlation

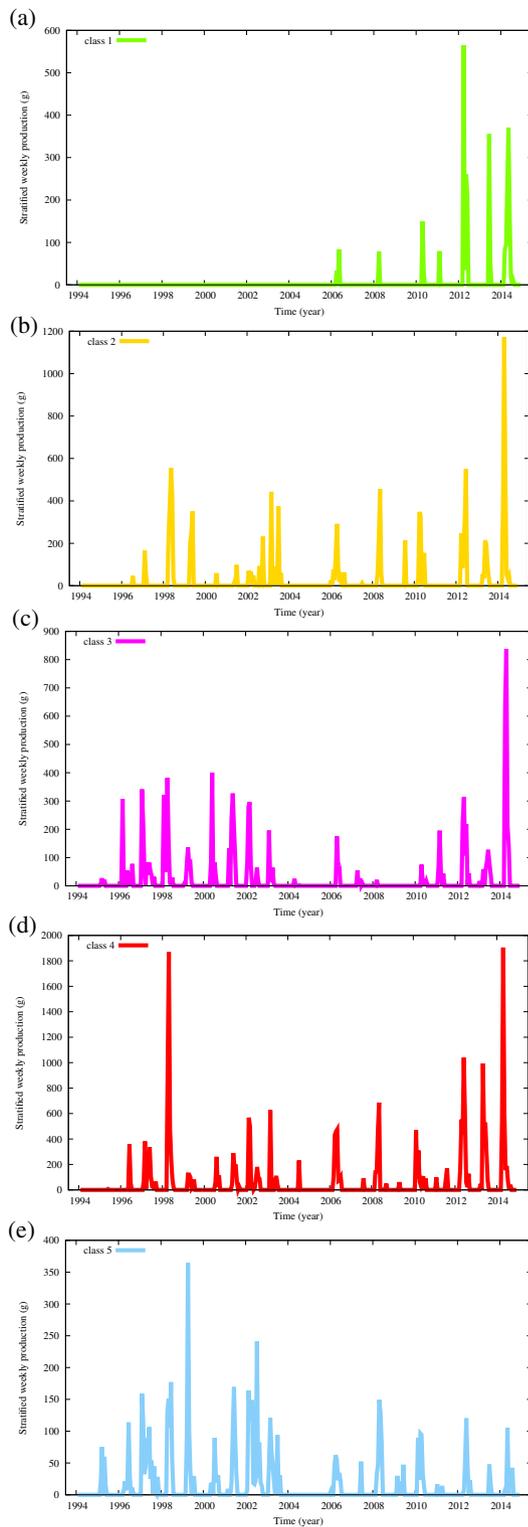


FIGURE 4 As in Figure 4 but segregated according to the age-class (a, b, c, d and e) corresponds to class 1, 2, 3, 4 and 5, respectively) [Colour figure can be viewed at wileyonlinelibrary.com]

amounts $r = .74$. Note that correlations values above .4 are statistically significant (see Section 3 for details). At monthly time scales, whole year (January to December)

correlation is $r = .70$ and the same holds for the production period. In Figure 6, inter-annual variability can be observed with 1996, 2000, 2001 and 2004 registering the highest amounts of precipitation. It is interesting to notice that these years do not coincide with years of maximum production as shown in Figures 2 and 4. Nonetheless, in Figure 6, it can also be seen that the years of maximum precipitation are not exactly the same when we look at the whole-year versus September-to-December amounts. This suggests that the dominant precipitation months are not necessarily within the production period, therefore, precipitation maxima as shown in Figure 6 are not necessarily coincident with the years of highest production of mushrooms. Notwithstanding, in a long-term frame, the first part of the measurements period is characterized both by higher precipitation and higher production confirming the hypothesis of higher amounts of precipitation favours the growth of fungi.

At monthly scales (Figure S3) the precipitation shows a higher mean value during 1995–2004 than for the period after, 2004–2014. This could be related to the larger sizes observed during the first half of measure period in Figures 2, 4, and 5.

In Figure 7, the weekly time series of temperature anomalies are shown. The correlation from January to December between both sites series is $r = .81$, higher, as expected, than in the case of precipitation. From September to December the correlation value between temperature at both sites is $r = .77$. At monthly scale, from January to December the correlation is $r = .72$ and $r = .71$ for the production period. Monthly anomalies (Figure S4) show a warmer period during the first part of the records and cooler temperatures later on. This can be better noticed in Figures 7a and S4a, where whole year temperature is represented, than in those showing only the production months (Figures 7b and S4b). Therefore, the first part of the instrumental period is characterized by a warmer/moister pattern that coincides with larger production in Figures 2 and 4.

SoilT and SoilM at each land plot have been represented in Figure 8 using a similar colour code as in Figures 1 and 2. As can be seen in Figure 8a, soilT_{mean} evidences seasonal variability with higher moisture levels during autumn and winter and drier soil during the warm season. Corresponding opposite-in-phase changes in SoilM_{mean} can be noticed in Figure 8b, as expected. It is worth mentioning that during 2013, all devices were replaced and, therefore, some issues regarding homogeneity of the data cannot be excluded. Nonetheless, Figure 8b evidences high variability of the levels of soilM variance if series at all plots are observed, with some series showing higher soilM values before 2013 but others showing comparable values as those after 2013. Therefore,

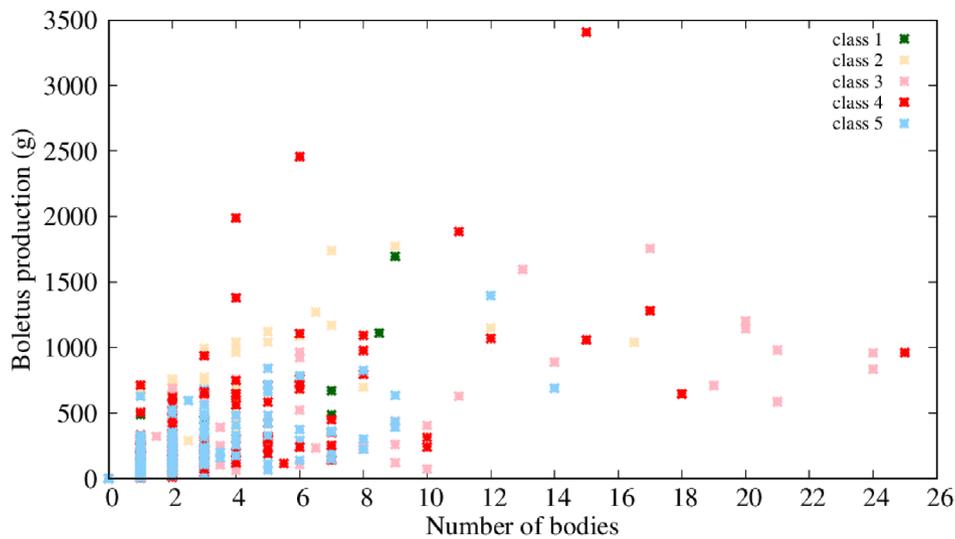


FIGURE 5 Number of *Boletus edulis* bodies versus their corresponding weight segregated according to the age classes ($p_{classes_i}$ with $i = 1, \dots, 5$ for the whole record period [Colour figure can be viewed at wileyonlinelibrary.com]

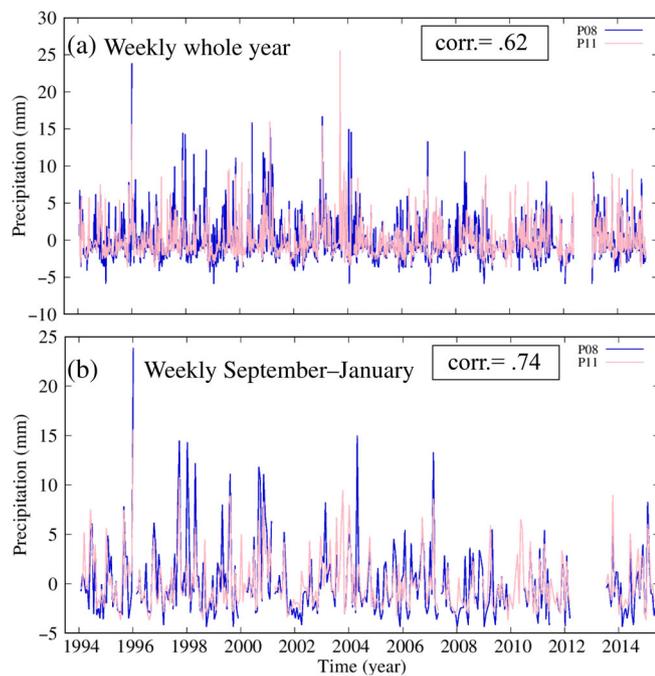


FIGURE 6 Weekly mean time series of observed precipitation anomalies w.r.t. the long-term mean for sites 2008 (P08) and 2011 (P11) for the whole year and only for the production season (September to December) in a) and b), respectively. Correlation values between series at the two sites are indicated in the corresponding panel (note that correlation values equal or above .4 are statistically significant at a 95th confidence level) [Colour figure can be viewed at wileyonlinelibrary.com]

although data prior 2013 should be interpreted with care, there are not enough evidences to reject these data. The differential radiation amounts received by each plot could at least partly account for these difference in soil moisture. However, differences in altitude can hardly explain this dependence on radiation since the differences in altitude among plots are of 50 m maximum. The

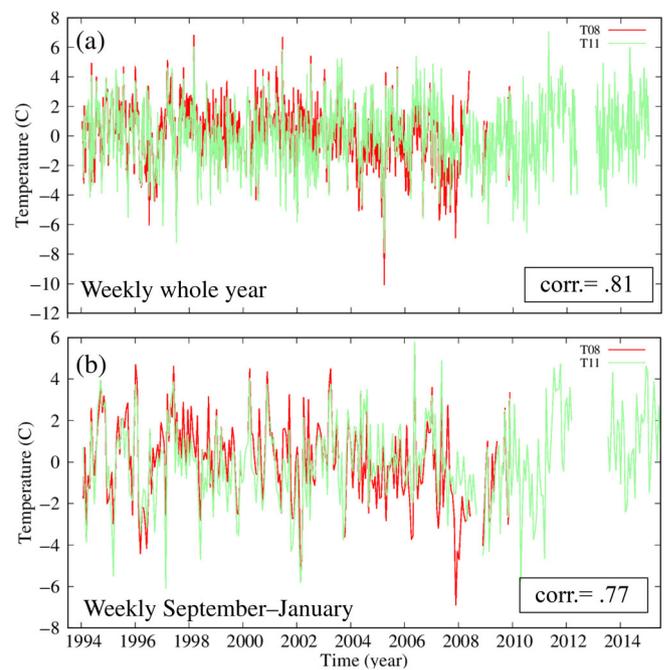


FIGURE 7 As in Figure 6 but for temperature [Colour figure can be viewed at wileyonlinelibrary.com]

vegetation cover nonetheless differs significantly from one plot to the other. For instance, some of the older plots present higher shadow rate due to the presence of taller and leafy trees. Therefore, if soilT has a certain influence on body fruiting, the radiation received at each one of the plots may have at least an indirect effect on fungal bodies emergence and growth.

On the other hand, soilM might have a relation of dependence with land inclination, due to the amount of water that at each plot is subject to run-off. These dependencies are explored in the Supporting Information. Figure S5a shows no large impacts of increasing plot

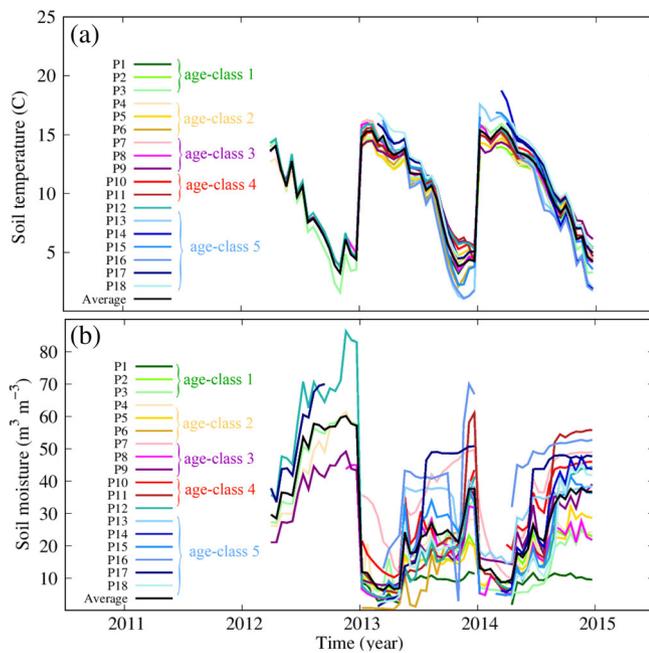


FIGURE 8 (a) September to December $\text{soilT}_{\text{mean}}$ for the period 2012–2014 at the 18 land plots (see legend for colours and age-classes) and averaged over all plots (black); (b) as in (a) but for $\text{soilM}_{\text{mean}}$ [Colour figure can be viewed at wileyonlinelibrary.com]

slopes on the weekly $\text{soilM}_{\text{mean}}$. The latter could be somehow expected since the sampling area was specifically selected for not having large terrain abruptness that could induce soil drying due to the mentioned run-off effects. Differences in altitude (Figure S5b) evidence as well a limited impact in SoilT .

In order to isolate the effect of trees age on the *B. edulis* production from that arising from climate variations, the stratified mean production (P_S) was selected to evaluate the influence of local temperature and precipitation on the fungi production. The production season usually starts around late September and beginning of October and finishes by late November or early December, depending on the year. This is a fruiting period (SOND) consistent with that described for *B. edulis* in several Central European taxonomic monographs (Moser, 1983; Breitenbach and Kränzlin, 1991) and experimental studies (Salerni and Perini, 2004), although some authors describe an earlier phenology (JAS) in more northern or cold climates (Pinna *et al.*, 2010).

Figure 9a shows the correlation (bars) between annual *B. edulis* production and temperature (T8 in purple corresponds to site 2008 and T11 in green, to site 2011) and also precipitation (P8 in blue and P11 in orange, for sites 2008 and 2011, respectively). Each group of bars shows the correlation for the annual time series calculated for a single month (SOND) and for several

months (SO, SON, SOND, etc., see Section 3). Production and precipitation/temperature series are synchronous in panel a) while Figure 9b–d show lagged correlations (lags = 1, 2 or 3 months, respectively).

Statistically significant positive correlations ($r \geq .4$) are noticeable between the mean stratified production P_S and the precipitation in September. It is also evident that lagged precipitation, especially for the case that includes August ($r \sim 0.6$ in Figure 9b) seems of relevance for the *B. edulis* production. However, this only holds at site 2011. Surprisingly, correlations with precipitation at site 2008 are negative instead or very low. It can be argued that precipitation amounts in September and previous months are still small to be representative of the precipitation regime over the area. It cannot be disregarded however that the different signs of the correlations values could be related with some problems with the quality of the instrumental data. Nonetheless, both precipitation series still correlate with a value of .70 with each other (see Figure 4), in both cases for the whole year and for the production season, which is a potential indicator that data might not necessarily be wrong at any of the stations. Instead, it can be said that single months correlation at both measuring sites can be variable, specially if specific months are considered, like September and lags, but this does not hold if aggregated values are considered.

In October, a significant role of precipitation is not supported by the correlation values (second group of bars in Figure 9, in opposition to what was observed for September (and its lags). Nevertheless, based on November and specially Dec correlations it seems that precipitation plays a prominent role (third and fourth group of bars in Figure 9a–d). The latter could indicate a mayor influence of precipitation at the beginning and the end of the production season. Correlation between P_S and precipitation in November + December is .64 (Figure 9b). For the extended production season (SO, SON and SOND and their corresponding lags), the role of precipitation does not seem obvious.

The role of temperature is apparently more limited than that of precipitation. This result is consistent with (Salerni and Perini, 2004) in Italy where it was found that the fruiting of *B. edulis* has a slight positive correlation with rain but not with temperature. It appears to be important for the mean production during the extended season SO and lags and also during the colder months later (Figure 9a), although again the relative contribution of temperature is not in agreement if correlations at the two different recording sites are compared.

The correlation values with P_B (number of bodies) has been as well calculated and it is represented in Figure S6. Correlations evidence similar behaviour as

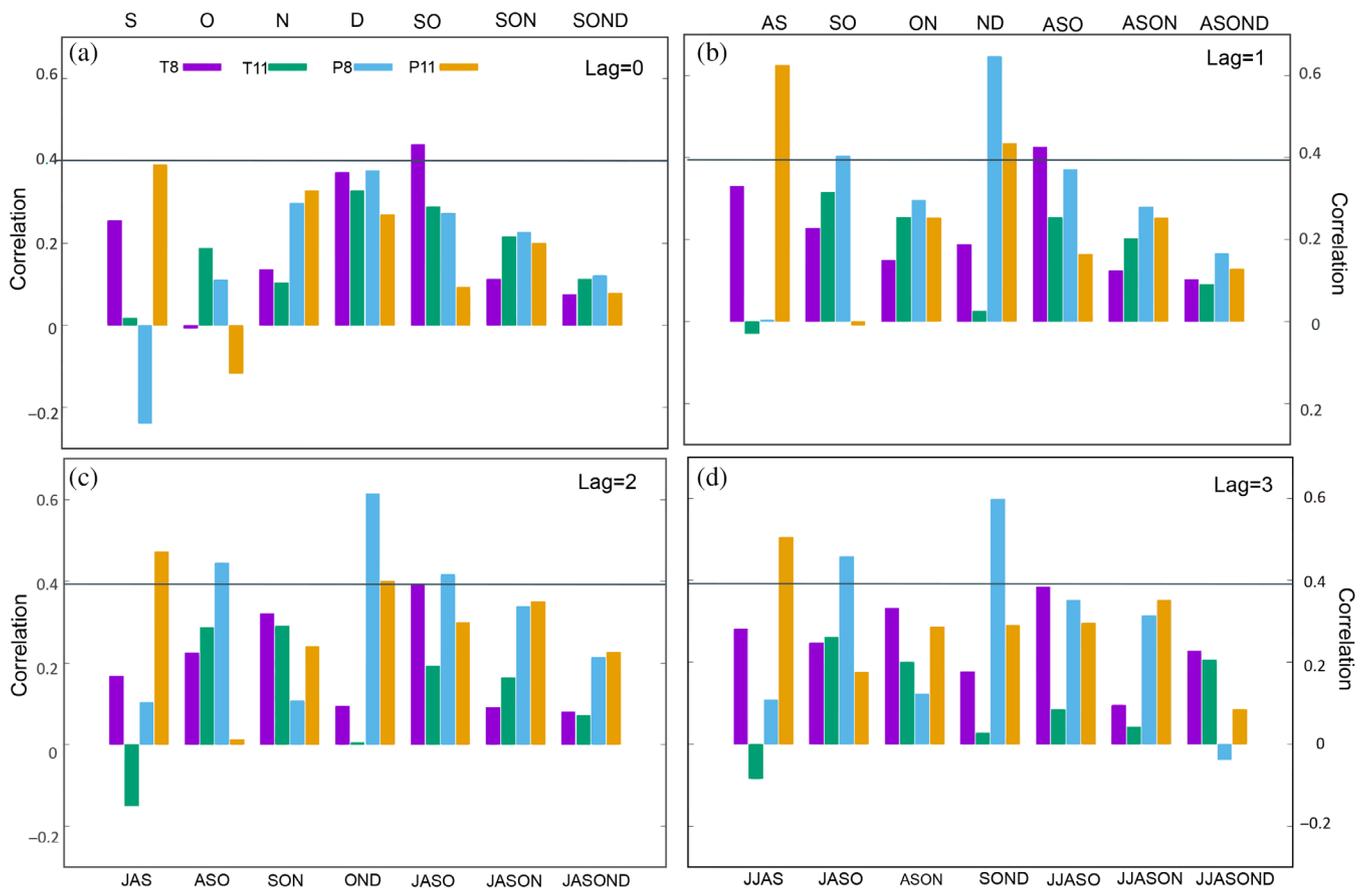


FIGURE 9 Correlation between annual *Boletus edulis* P_S and local climate variables: (a) correlation between P_S in September (S), October (O), November (N), December (D), September + October (SO), September + October + November (SON) and September + October + November + December (SOND) with temperature (T8 and T11) and precipitation (P8 and P11) at sites n° 2008 and n° 2011, respectively for the same months (lag = 0); (b) as in (a) but lag = 1 (1 month); (c) as in (a) but lag = 2 months; (d) as in (a) but lag = 3 months. The horizontal line indicates the 95th significance level for correlations [Colour figure can be viewed at wileyonlinelibrary.com]

with P_S , only for December the correlation cannot be taken into account because the number of bodies is very small. It may be also extrapolated that precipitation during the late part of the production season plays a more significant role in the number of fruiting bodies than in the total amount of fungi production.

4.2 | Link between the synoptic climate variability and *B. edulis* production

The correlation maps between P_S and the ERA-Interim reanalysis variables over the North Atlantic and European sector are shown in Figure 10 and Figure S7 of the Supporting Information. October production was chosen to show the correlation maps since the larger amounts of *B. edulis* production is usually found during the first weeks of this month. first column of Figure 10 shows the annual correlation maps between the mean

stratified production (P_S) and the annual series of 2mT, Pre_{Tot} , SLP and $SoilM_{L2}$ from the reanalysis fields only for October. In the second column of Figure 10 (first and second columns of Figure S7), the annual P_S in October is correlated with annual series from reanalysis averaged over SO with lag = 1 (ASO and JASO with lags 2 and 3, respectively).

2mT annual correlation maps (first rows in Figures 10 and S7) mostly evidence a positive correspondence with annual production over the domain in October, whereas the North Atlantic is dominated by negative correlation values. The latter implies that mild temperatures over the European continent intensifies the *B. edulis* production during October. If lagged correlations are considered including, therefore, the influence of temperature in the months previous to the onset of fungi production, cooler temperatures seem to gain relevance. Therefore, as it is shown in Figure S8, the negative correlations for September and before over the Iberian Peninsula,

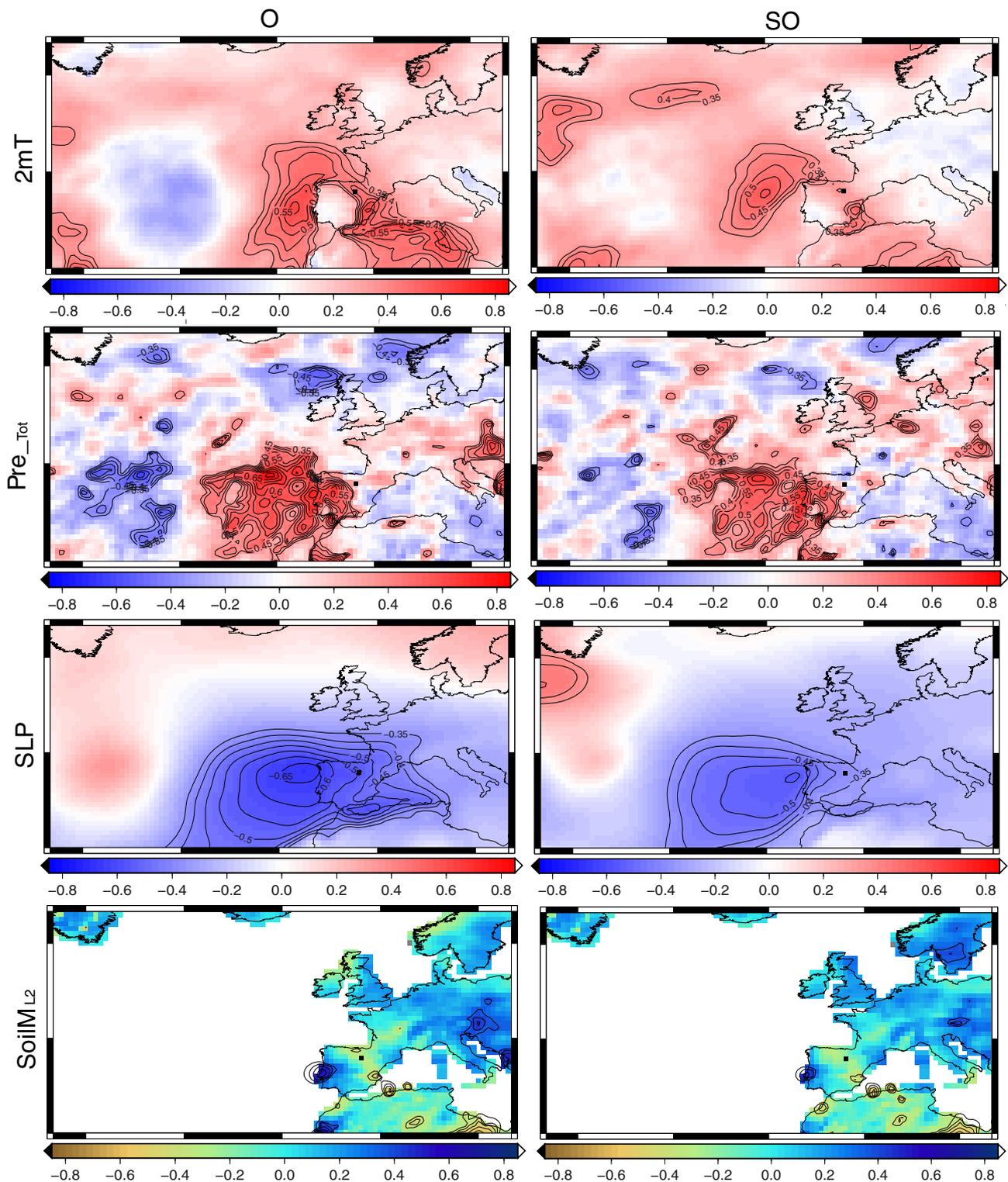


FIGURE 10 Correlation maps between *Boletus edulis* production in October and reanalysis variables. In the first row the correlation between P_S and 2mT ($^{\circ}\text{C}$); the second row shows the same but for Pre_{Tot} (mm); the correlation between P_S and SLP (mb) is shown in the third row and in the last row the correlation between P_S and SoilM_{L2} (m^3m^{-3}) is presented. In the first column, both production and reanalysis variables correspond only to October while in the second column the correlation between production in October and reanalysis variables averaged over September and October (SO) appears. Correlations equal or above .4 are statistically significant at a 95th confidence level and they are indicated by the contour lines. A black square indicates the exact location of the study region in Soria [Colour figure can be viewed at wileyonlinelibrary.com]

implying cooler summer conditions, seem to favour increased fungi production over the area of interest. Pre_{Tot} maps (second rows in Figures 10 and S7) show positive correlations over most parts of the Iberian Peninsula and at the north eastern Atlantic. Therefore, a wet autumn seems advantageous for mushrooms development. This pattern seems to be important also if September Pre_{Tot} is additionally considered (lag = 1), although in this case, a wetter Mediterranean would apparently ease the early *B. edulis* production (second row in Figure S8).

Correlation between SLP and October P_S (Figure S7, third row) shows negative associations over most of the north Atlantic domain. Therefore, consistently with the 2mT and Pre_{Tot} shown before, low pressures over this region would imply an strengthened production. The latter goes in hand with wetter summers over the region favouring the October *B. edulis* production, given that low pressure anomalies that might induce precipitation over the area, are also relevant if lagged correlations are considered.

Finally, fourth row of Figure S7 shows correlation between P_S in October and $SoilM_{L2}$ for the same month and also for various lags. Positive correlations can be observed when summer months (August and July) are considered but negative in autumn (September and October). Therefore, the *B. edulis* production in October is favoured by enhanced soil moisture during the warm season while drier conditions later support the production. This can be understood from the perspective of underground humidity playing a fundamental role in the warmer/summer part of the year. However, in a cooler environment, is the soil temperature who becomes the limiting factor, provided that the potential effect of freezing in the subsurface hampers the development of the fungal species.

Figures S8 and S9 consistently show preferential wet soil conditions during summer to enhance fungi production. Figures S10 and S11 additionally show the correlation maps for the production in November and the corresponding reanalysis variables in the same month plus the corresponding 3 month lags. Maps show a warmer eastern Mediterranean (2mT in the corresponding first row) with relatively cooler temperatures over the Atlantic and continental Europe. The pattern of precipitation (Pre_{Tot} in the second rows of Figures S10 and S11) indicates wet conditions all over the domain and dominating low pressures over Europe (SLP in the third row). A wet soil is also apparent over western Iberian Peninsula, but not particularly over the region of interest, specially if lags are accounted for ($SoilM_{L2}$ in the respective fourth row of Figures S10 and S11). All these evidences indicate, therefore, an explicit relationship

between mushroom production and large scale precipitation, specifically during the months prior to the onset of the fungi appearance connected to low sea level pressures and wetter soil conditions during the warm summer months and early autumn.

Figure S12 shows the annual correlation maps for the extended season (SOND) production and the averaged reanalysis variables over the same months. The accumulated production seems to be enhanced by mild temperatures (2mT in the first row) over most of the European region as well as wet conditions (Pre_{Tot} in the second row) and low pressures (SLP in the third row). A relation with wet soils seems also apparent over most of the peninsula, although as seen above, not particularly over the study region ($SoilM_{L2}$ in the fourth row). In addition, no large differences between stratified (left, P_S) and non-stratified (right, P_W) *B. edulis* production are noticeable. Nevertheless, it can be observed that correlation patterns are more pronounced in the case of P_S , indicating that solely the average that do not take into account the effect of age-classes might be less suitable to identify the influence of climatic factors on the production of fungal species, revealing thus a mixed signal with the role of the host tree ages on the emergence and growth of bodies.

It has been show that the large scale variability is to some extent connected with the *B. edulis* production, as expected. It would be interesting to examine if the large scale variability that has an impact on the production could be linked to any of the well-known circulation patterns over Europe and the Euro-Atlantic sector. Therefore, the correlation between P_S and the historical teleconnection indices specified in Section 3 has been calculated. Significant correlation has been found between the EA (.42) and the SCAND (.45) patterns and the late autumn (November and December) production. The positive phase of the EA mode is associated with milder winters and above-average precipitations. The SCAND pattern is responsible as well of more humidity over Europe in its positive phase. Those characteristics, higher temperatures and extra ground moisture, favour the production of this fungus species. Late summer conditions (September) potentially connected to the NAO and EAWR modes have also been found to present some connection with the *Boletus* production series. In particular, a negative correlation between production and the NAO time series has been detected (-.44). It implies a certain link with the negative phase of the NAO resulting in wetter and colder than normal summers over Europe. The latter, although takes place specially over the northern European regions might potentially impact the region under study. A similar impact of the positive phase of the EAWR pattern on the central and northern Europe climate may be related to the observed *B. edulis* production.

Therefore, it can be said that the correlation maps obtained within this section indicating how preferentially cooler summers and wetter autumns favour the *B. edulis* growth are consistent with the correlation evidenced between the main indices of circulation over the European sector and the mushroom production.

A number of studies coincide with the findings herein about the fundamental role of pre-season (late summer and early autumn) precipitation over large scale regions such as the whole Mediterranean sector (Alday *et al.*, 2017; Herrero *et al.*, 2019). The relative less important influence of large scale temperature, although non negligible and focused on the persistence of warm temperatures during the onset of the production season, is also highlighted by a few works (Tahvanainen *et al.*, 2016; Taye *et al.*, 2016).

4.3 | Influence of edaphoclimatic soil conditions on *B. edulis* production

Soil conditions are a fundamental factor that determine the capacity of the subsurface to generate the most beneficial prerequisites to ease fungi emergence and growth. Although manifold aspects related to the soil features take part in the process of mushrooms emergence, understanding at least partly the role of the soil temperature and moisture in the fostering/hampering of fungal bodies seems of central importance to evaluate the effect of climate variability on their development. In the previous sections a linear relationship between the fungi production and local as well large scale climate variability has been identified by exploring the correlation between the *B. edulis* production and various local and synoptic variables. It is also relevant to evaluate whether climatic factors can boost production or in the contrary to what extent they are responsible for the termination of the production season. Herein, we investigate in if particular instrumental values of soilM or soilT measured at each land plot can impose thresholds to the fungi growth.

Figure 11 shows the dispersion diagrams between P_w during the whole production season, from September to December, and the corresponding weekly soil variables. In the first row soilM_{mean} is represented while in the second soilT_{mean} appears. Maximum and minimum values are represented in the first and second columns, respectively of Figure S13 of the Supporting Information. Dots represent the weekly pair of values (P_w -soilM/soilT) for the 18 land plots with colour corresponding to the age-class (as in Figures 1 and 4). Production takes place within the range of soilM between 10 and 70 m³m⁻³ (Figure 11a). The largest P_w values are for soilM comprised within the interval 20–45 m³m⁻³. The most

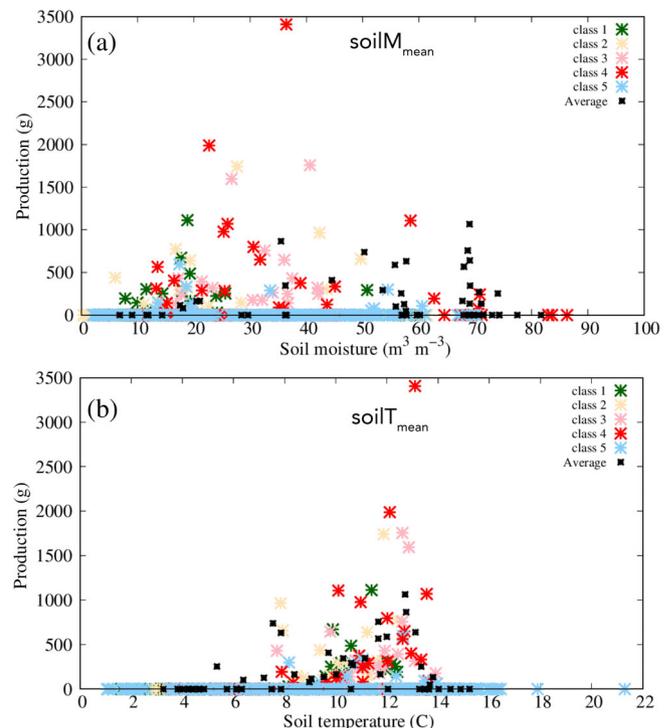


FIGURE 11 P_w versus weekly instrumental soil conditions. (a) P_w versus soilM_{mean} for weeks within September to December during the period 2012–2014. Colour stands for the corresponding age-class (see legend); (b) as a) but for soilT_{mean} [Colour figure can be viewed at wileyonlinelibrary.com]

productive age classes are p_{class_3} and p_{class_4} , consistently with what was shown in Figure 4. *B. edulis* sporocarp production is highly influenced by the *P. sylvestris* stand class age (Martínez-Peña *et al.*, 2012a). The higher production is in the fourth stand age class, between 51 and 70-years-old, which could be considered mature stands. Hintikka (1988); Keizer and Arnolds (1994) also found this species typical of mature pine stands. In particular, p_{class_4} is available as well for large soilM content (maximum value reached for this age class plot production at 90 m³m⁻³). It is noticeable that p_{class_5} , the production related to the oldest pine plots emerge for low soilM_{mean} values. For soilM_{min} and SoilM_{max} values in Figure S13 the production expands the ranges to 5–90 m³m⁻³, however limited to smaller amounts. In general, it can be said that younger pine hosts tend to produce under drier soil conditions than required in the case of older trees.

SoilT_{mean} values (Figure 11d) show that apparently the adequate range of subsurface temperatures for production oscillates between 8 and 14°C. Maximum production takes place around 12°C. Similarly, as in the case of soilM, if soilT_{min}/soilT_{max} in Figure S13 are considered, the temperature range expands to larger intervals although we also found that the production amounts is limited comparatively to soilT_{mean} values. The differences in production according

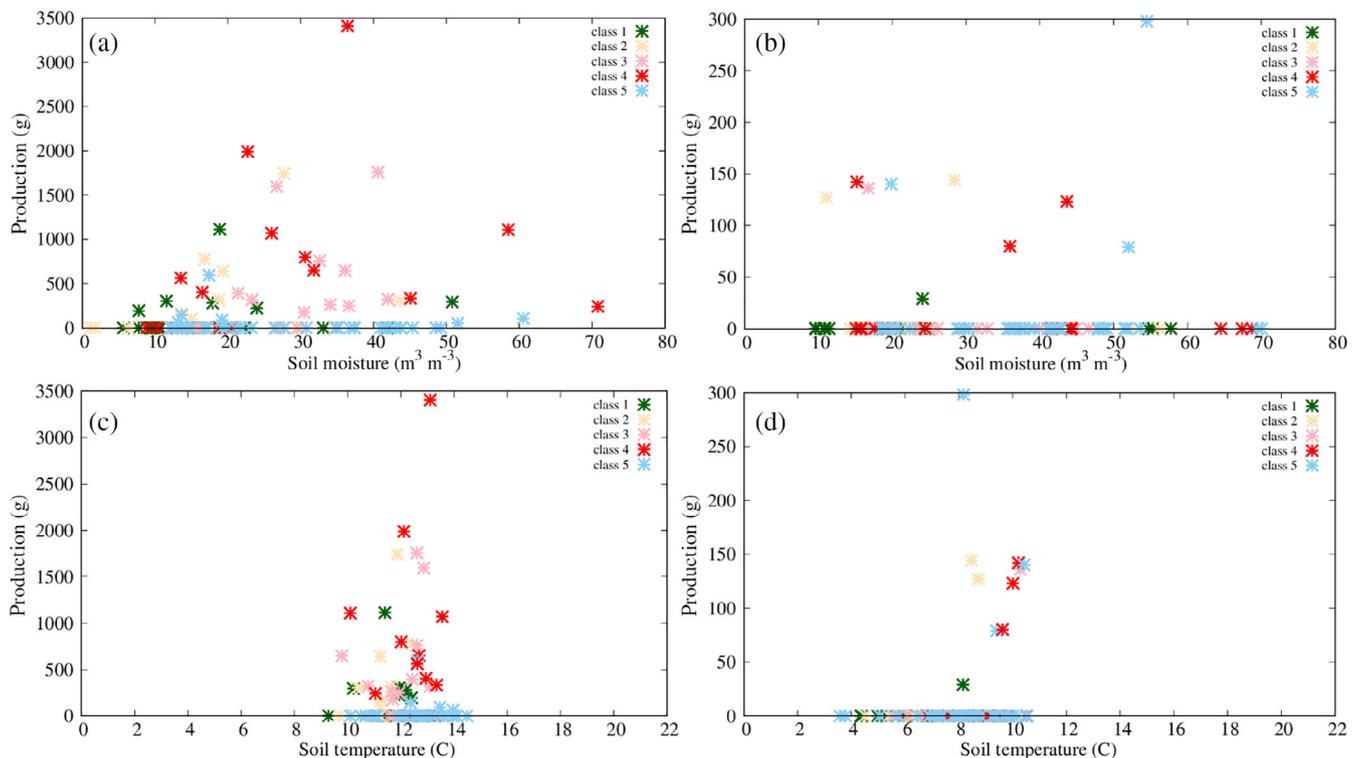


FIGURE 12 P_w versus weekly soilM_{mean} ($\text{m}^3 \text{m}^{-3}$, first row) and weekly soilT_{mean} ($^{\circ}\text{C}$, second row) for the three initial (final) weeks of the production season in the left (right) over the period 2012–2014 from September to December. Colour indicates age-class. Note the different scales of each panel [Colour figure can be viewed at wileyonlinelibrary.com]

to the age-classes that were apparent in the case of the soilM are hardly noticeable for the soilT conditions. This can be better appreciated in Figure S14, where a dispersion diagram between production at the different land plots and the corresponding soilM and soilT values segregated according to the age-class has been represented.

In order to explore what are the soil conditions that foster or hamper the initiation/termination of the *B. edulis* production season, an analysis focused only in the first/last production weeks has been performed. In particular, the first three (41, 42 and 43) as well as the last three (46, 47 and 48) production weeks are considered for such analysis. Figure 12 represents dispersion diagrams as in Figure 11 but only for the selected weeks. In the case of soilM, the production tends to start within a range between 10 and 50 $\text{m}^3 \text{m}^{-3}$ (Figure 12a). Although a few values also appears around 60–70 $\text{m}^3 \text{m}^{-3}$. More interestingly, Figure 12a evidences that maximum production occurs at the beginning of the production season (early to mid October). Similarly, from Figure 12c, it can be inferred that a narrow range between around 10–13 $^{\circ}\text{C}$ of soilT favours the growth of the largest amounts of *B. edulis* in this area. Therefore, the major contribution to the total production takes place during the early onset of the season. The decline of the production amounts is very obvious when the last 3 weeks of the production season

are considered in Figure 12b,d. The production decreases below 500 g/week in ranges from 10 to 50 $\text{m}^3 \text{m}^{-3}$ and a smaller soilT range (8–10 $^{\circ}\text{C}$), revealing the role as limiting factor of the soilT in the termination of the production season. Apparently, the soilT plays a more pivotal role than soilM in the ending of the production period. According to Karavani *et al.* (2018), at the end of the season (November–December), when rainfall and the availability of water in the soil are sufficient for the fruiting of the fungi, production is more limited by low temperatures. Likewise, Hernández-Rodríguez *et al.* (2015) find that the low temperatures in these months may be related to the decrease in mushroom yield. SoilM, however, does not evidence a large influence on the season initiation, but this can also be related to the limited amount of data and potential quality issues. This result contrasts with Pinna *et al.* (2010) showing how high average soil moisture promotes early fruiting of *B. aff. edulis* in Canada. Likewise, Hall *et al.* (1998) and that *B. edulis* fruiting in Europe can even be inhibited during very dry summers.

5 | CONCLUSIONS

In this work, the link between climatic factors and *B. edulis* production over a region at the north eastern

Iberian Peninsula (*Pinar Grande* in Soria) during the period 1995–2014 has been investigated. The first insights allowed to establish a relationship between the weight and the number of fungal bodies. Apparently, larger mushroom bodies do not necessarily imply larger amounts of production in weight, on the contrary, it seems to act as a limiting factor, that is, the larger the fungal bodies, the lower the total number of bodies produced. There are evidences from the recorded production that the largest contribution to the total amount of *B. edulis* produced is associated with the mid age host trees. We have found, however, a limited impact of the height or slope of the corresponding land plots although a certain dependence on the vegetation cover that determines the amount of radiation at each plot can be detected and, therefore, an influence on the retained humidity in the soil.

The climate variability during the observational period is seemingly segregated in two differentiated periods. During the first half wetter and to some extent also warmer conditions prevailed if compared to the last 10 years. The latter would have enhanced the *B. edulis* production from 1995 to 2004. Local observed climatic data evidence that precipitation at the onset of the production season is of special relevance as well as during the previous months (summer). However, the observed surface temperature do not reveal an obvious influence on the *Boletus* production. The surface temperature effect during the colder months late in the production season is also detectable. Precipitation does not seem to be important however at the end of the season, although it somehow has a certain relevance specifically for the number of bodies (P_B) and also if the lagged (accumulated) precipitation totals are considered. Nonetheless, although the precipitation and temperature time series between at the two meteorological stations are to some degree correlated, the information provided by the two sites illustrates as well some contradictory impacts on fungi production. Therefore, further insights from a more regional/synoptic perspective, avoiding so a focus on too local features was pertinent.

It has been shown that mild surface temperatures in autumn over the European and north Atlantic sector and cooler conditions during the preceding months over Europe help enhance *B. edulis* production. A relation between fungi production and the prevalence of wet summers until the onset of the production season has also been identified, which was linked to the presence of anomaly low pressures over the Atlantic area. It has been also detected that for the early production it is of certain relevance a wet Mediterranean region during the late summer. The latter was evidenced by positive correlations between the precipitation amounts and *B. edulis* production over the Mediterranean during the onset

months and their corresponding lags, suggesting that more humid summers over western Europe are aligned with a wealthier production season. The associations found between the *Boletus* series and the teleconnection indices are consistent with the large scale features suggested above based on the correlation maps for the Euro-Mediterranean area.

With respect to the large scale soil conditions, humid soils all over the Iberian Peninsula during the summer benefit the growth of fungal bodies, although the peak of the production season apparently does not demand a particular wet soil. The rest of the production season prior the winter acknowledges wetter soil conditions. In general, the whole season production (SOND) seems to be favoured by humidity and warmth.

Regarding local soil conditions related to the production at *Pinar Grande* the production falls well within a soil moisture range of 10–70 m^3m^{-3} and soil temperatures between 8 and 14°C. It has been identified that this is however affected by the age of the pines that serve as host for the fungi species. In particular, higher soil moisture is required for older trees. Therefore, the influence of the biological issues, as the age of trees, plays a role in the growth and production of *Boletus* in the area, along with the climatic influence. Larger production takes place at the beginning of the season for intermediate values of soil moisture (20–50 m^3m^{-3}) and soil temperature (10–13°C). Therefore, large humidity or too cold/hot temperatures do not generally favour fungi growth and production. Thus, we can consider that a limiting factor for the initiation of the production season is an adequate soilM at the beginning while low soilT characterizes the termination of the season.

Further research would benefit this type of studies. For instance, modelling studies with high spatial resolution simulations would be helpful to understand processes and mechanisms of interaction between climate variability and the growth of fungal species over the Iberian Peninsula.

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ENDNOTE

¹ MICODATA 2005–2006 Report. DIEF Valonsadero (<https://coleccion.es.gbif.es/public/show/in22?lang=en>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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