School of Agrifood and Forestry Science and Engineering (ETSEA)

Conditional Yield Models for Edible mushrooms in Pinus pinaster stands of Soria province, Castilla and León region, Central Spain

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A thesis submitted to School of Agrifood and Forestry Science and Engineering in Partial fulfillment of the requirements for the degree of masters in Mediterranean Forestry and Natural Resources Management (MEDfOR)

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Abstract

Integration of non-wood forest products (NWFPs) into forest management planning has become an increasingly important issue in forestry over the last decade. Mushrooms are among the valued NWFPs due to their medicinal, nutritional, commercial and recreational importance. Commercial mushroom harvesting and local tourism through mushroom collection also provides important income to local dwellers and contribute to the economic value of regional forest and could act as an incentive for sustainable forest management. The sustainable utilization of the potential in mushrooms in a region requires generating information on their occurrence and predicts their yield. In this study we have used a two stage modeling approach coupled with mixed-effects modeling to separately model the probability of occurrence and conditional yield of edible, marketed and *Lactarius* group *deliciosus* mushrooms in *Pinus pinaster* forests in Soria, Central Spain. We used climatic, soil and stand characteristics. The best logistic regression models for predicting probability of occurrence of edible, marketed and *Lactarius* group *deliciosus* mushrooms are mainly based on autumn precipitation having a positive effect. For *Lactarius* group *deliciosus*, pH has also been a significant predictor, and inversely related with occurrence of mushroom. In the best conditional yield models stand (age of oldest tree) and soil (soil textural class) characteristics became important predictors as we move from the general edible group to marketed and genus level, *Lactarius* group *deliciosus.* An increase in stand age and sandy soil textural class showed a negative effect. Not only the amount of rainfall but also its distribution affects mushroom yield. The modeling approach we used is advantageous since it enable us to examine the effect of the predictors on the occurrence and the yield of mushrooms separately which could help to better understand the system. In addition, the results of the two models can be combined to get the predicted mushroom yield under specific conditions.

Key words: Edible, *Lactarius* group *deliciosus,* marketed, mushroom, mixed-effects, non-wood forest products (NWFPs), two-stage modeling.

1. Introduction

Forests, in addition to the direct wood products, provide diverse ecological services and resources for society. They are habitat for animals, play significant role in water cycling and soil development, provide resins, oils, mushrooms etc, plus they are used as a hunting and recreational place. Mediterranean forests are recognized for the diversity of both wood and non-wood forest products (NWFPs). The most valuable NWFPs from these forests include pine nuts, cork, edible fungi and resins (Bravo *et al.*, 2011).

Wild edible fungi have obtained significant attention as one of NWFPs due to the observed potentials. At a global scale, it has been indicated as there are 2166 species of wild edible mushrooms of which more than 470 have medicinal properties. This shows the economic importance of the mushrooms and their relevance as food source (Boa, 2004). In Spain, according to Marraco and Rubio (1992) (as sited in Ortega and Martínez-Peña, 2008) the revenue from mushroom collection is approaching the return typically expected from timber which had been consider the most important resource from the forests in this country. Specifically, in a study conducted in Castilla y León, Martínez-Peña *et al*. (2007) has indicated the average annual production of wild edible mushrooms of social and economic interest was estimated to be 34,000 tones (excluding Tuber genus) produced in an area of 4.5 million hectares. Similar study showed as 54% of the population in Castilla y Leon picks mushrooms implying a potential of 567,715 local harvesters. This potential capacity indicates the possibility to generate up to 65 million Euros by marketing the main commercial species. Some fungi such as boletes (*Boletus edulis*) and saffron milk caps (*Lactarius* group *deliciosus*) are specially valued in many countries, and their trade has become an important complementary economic activity in many regions (Voces *et al*., 2011; Cai *et al*., 2011; Martínez de Aragón *et al*., 2011).

Bonet *et al*. (2014) also demonstrated the importance of mushroom productions in Catalonian pine forests with 24,500 tons/yr of mushroom of which 14,300 tons are edible and 7.900 tons are commonly marketed mushrooms. The corresponding economic value is estimated to be 48 and 32 million Euros for edible and marketed mushrooms respectively (Bonet *et al*., 2014). Some studies have also showed that the market demand for many ectomycorrhizal fungi has increased to the extent that commercial value of forest fungi may equal or even surpass the value of timber (Alexander *et al*., 2002; Arnolds *et al*., 1995; Palahi *et al*., 2009).

A survey conducted in Catalonia demonstrated that the residents are willing to pay for the experience of picking mushrooms (Mogas *et al*., 2005). Hence, in addition to acting as a source of income and tourism business mushroom could soon provide incentive for the forest landowner for improved forest management. This could lead to shift in management priorities and interventions such as thinning, pruning, and control of invasive plants. These management priorities would become more apparent in a frequent basis when mushrooms provide revenues for forest managers. This would also have implications in making forests less vulnerable to wild fire and over grazing (Bonet *et al*., 2008).

These potentials that could be harnessed from wild edible mushroom coupled with other factors like the decrease in the profitability of wood production is making forest and land manager to seriously evaluate the importance of many NWFPs like mushroom (Mogas *et al*., 2006). Pilz and Molina (2002) also indicated that the potential in mushrooms has triggered a growing interest from forest owners and managers to inventory, predict, and develop the commercial mushroom production.

In order to have a sound forest planning for a joint production of wood and mushrooms requires prediction of both mushroom and wood production (Palahi *et al*., 2009). This requires detailed information on the main variables affecting mushroom yield. Several factors affecting mushroom yield and dynamics have been indicated in the literature. These factors are classified into three main groups; which are stand structure (e.g. tree species, stand density, stand age), weather variability (e.g. precipitation, temperature) and local site characteristics (e.g. altitude, slope, aspect) (Martínez-Peña *et al*., 2012a). For example, for the species that establish mycorrhizal symbiosis with trees, it may be expected that stand structure which can be modified through forest management, as well as soil properties affect mushroom production. It is also well known that weather, together with other environmental factors, also affect mushroom dynamics. In addition, the local site characteristics have been repeatedly mentioned in the literature to have an impact on mushroom yield (Egli, 2011). The presence of large amount of potential variables related to mushroom productivity and their interdependence makes it difficult to give clear recommendation for managing mushroom yields there by making yield prediction not an easy task. Systematic quantitative analyses on the effect of different variables are required (Martínez-Peña *et al*., 2012a).

Modeling techniques are a valuable tool that allows identifying factors most relevant for predicting mushroom yield. Forest management oriented models based on long historical data series of annual measurements in many locations can be used to model mushroom yields as a function of different types of predictors. In general there are very few models in the literature to predict production of NWFPs for use in forest planning (Bravo *et al*., 2011). These kinds of studies are rather recent, and only a few models for mushroom yield have been published so far. Bonet *et al*. (2008) developed a model for predicting the total edible and marketable mushroom yield and species richness as a function of site and forest stand variables based on a three year mushroom inventory in 24 Scots pine plots in north-eastern Spain. In this study they showed that basal area was the most important growing stock characteristics for mushroom production with maximum mushroom yields at stand basal areas of approximately 20 m^2/ha. Additional study based on 21 plots established in *Pinus sylvestries*, *Pinus nigra* and *Pinus halepensis* forests in the same region also found that maximum mushroom productivity corresponded to stands where the basal area ranged from 15-20 m^2/ha. Site variables such as aspect, slope and elevation also had an important influence on annual mushroom yield (Bonet *et al*., 2010). Martínez-Peña *et al*. (2012a) also developed empirical models for ectomycorrhyzal mushroom with special emphasis on most valuable species in the area in Scot Pine forest in North-Central Spain. They have found out that weather variables like rainfall and temperature have significant effect on mushroom yield and from stand variables dominant height, basal area and stand age have a significant effect.

As highlighted above, the presence of multiple factors responsible for high temporal variation in mushroom productions like variations in precipitation, temperature, frost, evapotranspiration, relative humidity, and water deficits (Martínez de Aragón *et al*., 2007; O'Dell *et al*., 1999; Straatsma *et al*., 2001) necessitates the collection of large quantities of data over several years for the construction of reliable models. The between region difference in site characteristics, weather and forest structure prevent straightforward application of the above mentioned results to other areas.

Traditionally resin was the main product of the *Pinus Pinaster* (Maritime Pine) forest in our study area, Southern province of Soria, Castilla and León region, in Central Spain, but the decline of its market in the 1970s led to a shift towards wood production. Recently, mushroom harvesting has become a major activity (Fernandez-Toiran *et al*., 2006). In recent years, associated with the increase of resin price these forests have again started to be exploited for resin as well. The aim of the study was to develop conditional yield models for predicting the production of mushrooms in Maritime Pine forests in Central Spain based on mushroom production data from seventeen consecutive years (1997-2013). The predictive variables tested include annual precipitation, monthly precipitation from August to November, mean annual temperature, mean monthly temperature from August to November, pH, percentage of organic matter, soil texture and age of oldest tree in the plots. A two stage modeling (Welsh *et al*., 1996; Fletcher *et al*., 2005) coupled with mixed-effects modeling technique was used to account for random annual variation of mushroom productions. The two-stage modeling approach allows us to separately model the occurrence of mushroom and yield given presence. Two-stage modeling has been recommended for data like mushroom production where we could get zero values in plots and also across year (Welsh *et al*., 1996; Fletcher *et al*., 2005). These models could support forest managers to optimize economic returns by predicting potential productions of mushrooms. They could also be used to support the local mushroom pickers as well as the truism linked to mushroom picking. In addition, coupling the output of these kinds of studies with evaluation of the local species for bioactive compounds could pave a way for attracting and integrating industrial innovation with the forest management planning.

2. Material and methods

2.1. Study area

The study area is located in the Southern province of Soria, Castilla and León region, in Central Spain in the so called “Pinares Llanos Centrales” area. Altitude ranges from 1000 to 1200 m.a.s.l. and annual rainfall ranges between 500 and 700 mm, with a marked summer drought. Average annual temperature is 10 °C, with cool winters (average January temperature is 2 °C). Soils are arenosols and regosols developed over tertiary and quaternary sands.

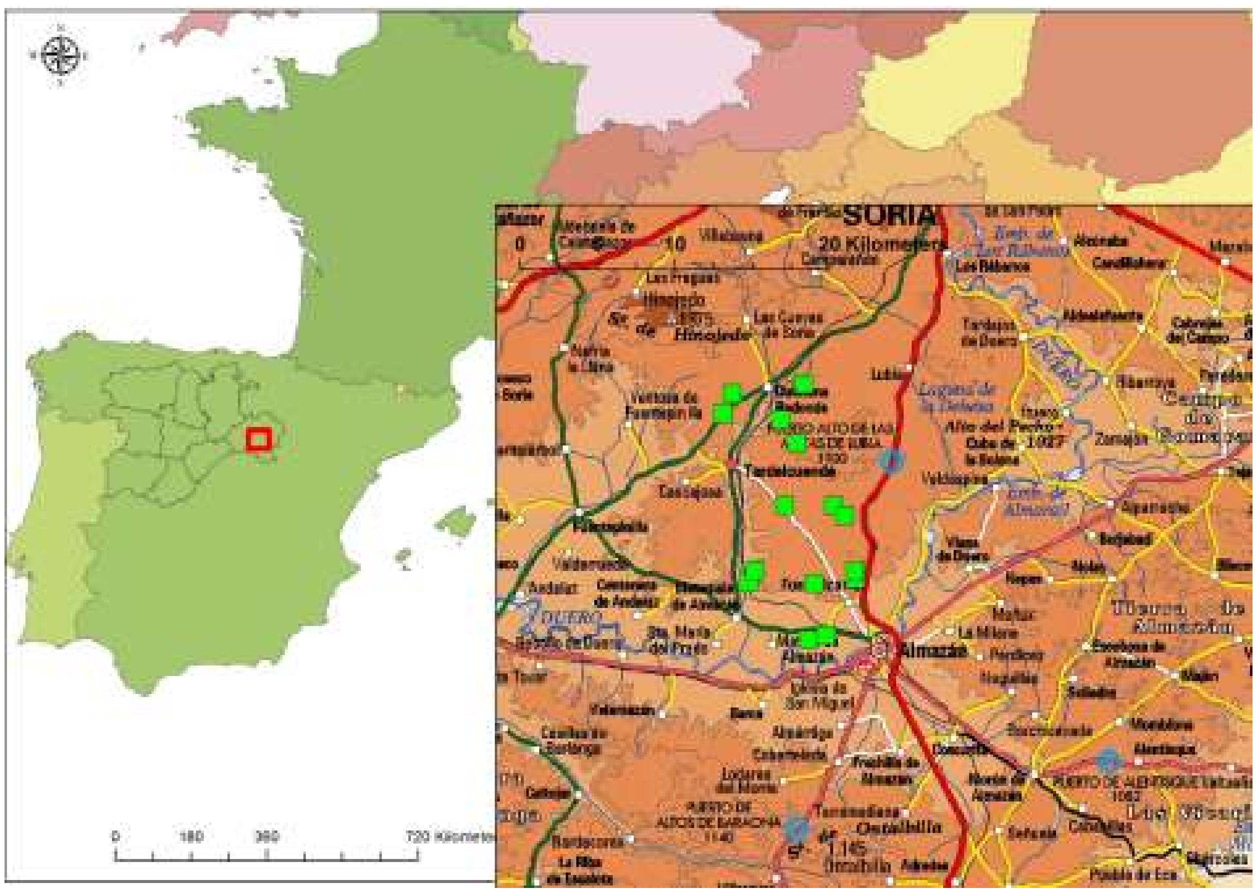

Figure 1. Map of the Study area

The original vegetation is mainly of *Quercus pyrenaica* Willd forests, which were converted into *P. pinaster* forests. Understorey is formed by different shrubs (*Cistus laurifolus* L., *Juniperus communis* L., *Erica arborea* L., *Calluna vulgaris* L.) and *Q. pyrenaica* resprouts. The rotation of *P. pinaster* is 80 years, with trees being cut into two phases. At the beginning of this research, most of the trees were removed at the end of the cutting cycle, whereas some were spared, as parent trees, for ten more years in order to provide seeds for natural recruitment. If natural regeneration was not successful, manual planting is conducted. Similar management schemes have been performed for the last century in the study area. Nowadays, the forests are silviculturally managed by clear cutting with soil harrowing and sowing.

2.2. Sampling design

The forest in the study area is a managed forest and the study plots were established as stated in Fernandez-Toiran *et al*. (2006) and Ágreda *et al*. (2013). We modified the age class based classification used by the previous authors to account for the long year data and possible change in age class. Based on age (the number of rings) of each tree in all plots determined in 2012, mean age and oldest tree in the plots were assigned for the whole study period, 1997 to 2013. Figure 2 shows the age distribution for each plot.

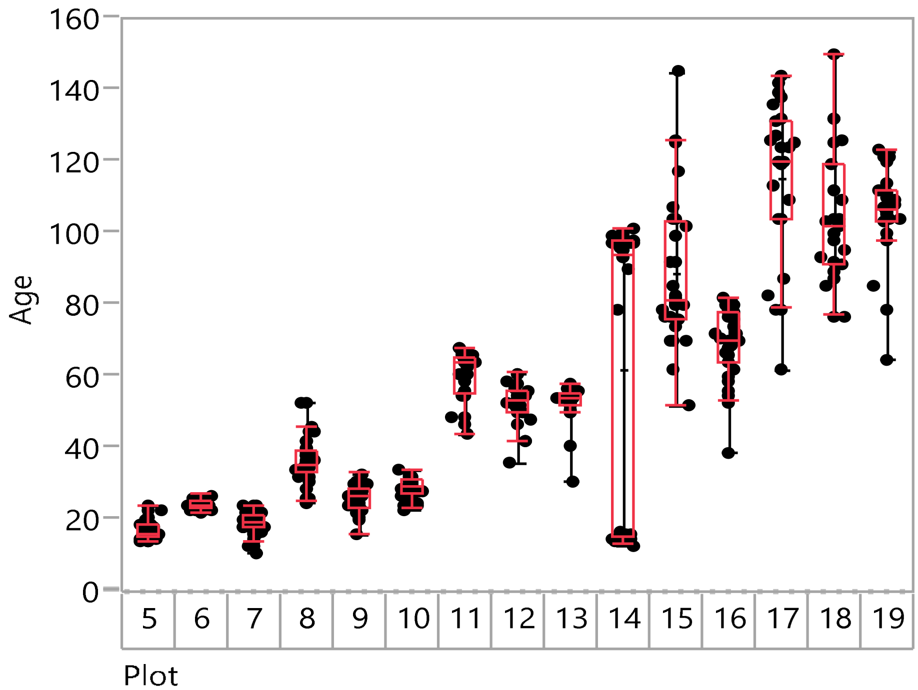

Figure 2. Age variability chart for each plot used in modeling

A total of 15 sampling plots were used for this study. Each sampling plot covers an area of 150 m^2, with a rectangular shape (5×30m). Plots were fenced to prevent harvesting and trampling. Plots were also made to be at least 500 m from stands corresponding with another age class in the forest management plan and areas with another tree species present were avoided.

Soil texture, soil organic matter and soil pH were determined for each plot at the beginning of the study. Weather data is obtained from a nearby meteorological station (23 km) from the study plot located at 414630 latitudes and 22859 longitudes (30T542963; 4624924). Since the study plots are located in a plateau we consider the weather data from this meteorological station very well represents the reality of the mushroom plots.

Sampling was performed from September to December (week 35–50) on a weekly basis from 1997 to 2013 since this period corresponds with most of the sporocarps' emergence; maximum production time being in October and November. All the sporocarps were collected, and the species were determined using morphological features with appropriate keys and monographs as described in Fernandez-Toiran *et al*. (2006) and Ágreda *et al*. (2013). Table 1 presents the species identified in this study. The study area is almost uniform and there was no much difference in slope and aspect of the plots (Majority with a slope of zero and with max slope value of 1.4 for some).

Table 1. List of edible and marketed species identified (species with * are marketed species)

Edible and marketed mushrooms identified in the study		
Agaricus impudicus	*Rhizopogon roseolus*	*Tricholoma ustale*
Agaricus sylvaticus	*Rhodocollybia butyracea*	***Hygrophorus agathosmus****
Amanita citrine	*Russula albonigra*	***Lactarius deliciosus****
Astraeus hygrometricus	*Russula caerulea*	***Lactarius sanguifluus****
Baeospora myosura	*Russula cessans*	***Lactarius semisanguifluus****
Chroogomphus rutilus	*Russula chloroides*	***Macrolepiota procera****
Cortinarius delibutus	*Russula heterophylla*	***Pleurotus eryngii****
Hygrophoropsis aurantiaca	*Russula risigallina*	***Suillus luteus****
Hygrophorus gliocyclus	*Russula roseipes*	***Richoloma portentosum****
Laccaria laccata	*Russula turci*	***Tricholoma terreum****
Lactarius chrysorrheus	*Russula vesca*	
Lycoperdon perlatum	*Russula violeipes*	
Lyophyllum fumosum	*Russula xerampelina*	
Macrolepiota konradii	*Suillus bellinii*	
Mycena galericulata	*Suillus granulatus*	
Mycena pura	*Tricholoma fracticum*	

A total of 42 edible mushroom species have been identified, of which non-marketed and marketed are represented by 33 and 9 species respectively. *Lactarius* group *deliciosus* is represented by three species out of the nine marketed species; these are *Lactarius deliciosus, L .sanguifluus,* and *L. semisanguifluus* (Table 1). The maximum edible, marketed and *Lactarius* group *deliciosus* mushroom production in our data set are 360.47 kg ha^{-1} yr^{-1}, 308.64 kg ha^{-1} yr^{-1} and 303.95 kg ha^{-1} yr^{-1} respectively; all were observed in 2012. Majority of the marketed mushroom is represented by *Lactarius* group *deliciosus* (76.12 %) (Table 2).

Table 2. Average mushroom production data and number of plots (N) used in conditional yield modeling

Production	Mean	SD	Minimum	Maximum	N	Percent
Edible(kg ha^{-1} yr^{-1})	32.26389	43.0342	0.03	360.47	220	
Marketed(kg ha^{-1} yr^{-1})	20.64148	33.2842	0.13	308.64	155	**45.15 %** of Edible
***Lactarius* group *deliciosus* (kg ha^{-1} yr^{-1})**	20.64008	35.11	0.59	303.95	118	**76.12 %** of Marketed

2.3. Modeling

There were three soil textural classes; hence, we created two dummy variables representing loamy sand and sandy loam texture respectively. Thus, sandy soil texture was used as the 'reference' or 'default' category.

Due to the zero-inflation of our data and after preliminary analysis I have decided to use a two-stage modeling approach (Welsh *et al.*, 1996; Fletcher *et al.*, 2005) in order to model the occurrence (presence or absence) and the positive abundance of mushrooms separately. For this, I have divided the data set into two. The production data for the edible, marketed and *Lactarius* group *deliciosus* (which include the species *L. deliciosus*, *L. sanguifluus* and *L. semisanguifluus*) were converted into binary data; 1 wherever there is production otherwise 0. I filtered out all the data with production value of 1 as a second data set. The binary data was used to fit logistic regression model for the probability of mushroom occurrence (Eq. 1). The second data set aimed at modeling the mushroom yield (fresh weight) conditional on the probability of mushroom occurrence (Eq. 2). The final yield equation would be a multiplication of the two models (Eq. 3). The equations are given below:

$$p(y) = \frac{1}{1+e^{-(\beta_O+b_O+\beta x)}} \qquad \text{Eq. 1}$$

$$ln(yield_c) = \alpha_0 + a_0 + \alpha x + \varepsilon \qquad \text{Eq. 2}$$

$$yield = p(y) \times Snowdon \times e^{ln(yield_c)} \qquad \text{Eq. 3}$$

where $p(y)$ is probability of occurrence of edible, marketed or *Lactarius* group *deliciosus* mushrooms, $yield_c$ is edible, marketed or *Lactarius* group *deliciosus* mushroom yield conditional on mushroom occurrence, $yield$ is edible, marketed or *Lactarius* group *deliciosus* mushroom yield (kg ha^{-1} yr^{-1}), α and β denote fixed-effects model parameters, a_0 and b_0 denote year random effects, x is a vector of independent variables, Snowdon is Snowdon's correction factor for the back-transformation bias (Snowdon, 1991), and ε is residual following a normal distribution with mean equal to zero and variance equal to σ^2.

The predictors used are presented in Table 3 below and can be categorized into climatic, soil and stand variables. In addition different combinations of the predictors were also used. For example Sum of different combination of the monthly precipitation and temperature. Transformations (logarithmic and square root) of the predictors were also evaluated for significance. We made sure about the correctness of the values recorded for mushroom production, hence, we considered all the values as real data and none were considered as being outlier.

Table 3. Predictors used in modeling.

Category	Predictors
Climate	P_ag, P_set, P,oct, P_nov, P_annual, (and different combinations)
	Tm_ag, Tm_set, Tm_oct, Tm_nov, Tm_annual mean(and different combinations)
Soil	pH, OM, Texture class
Stand	Plot Mean Age, Oldest tree in the plot

Where: ag, set, oct and nov stands for the months of August, September, October and November; OM for Organic matter (%),

The modeling data were characterized by multiple measurements for each individual sampling unit (i.e. repeated observations for the same plot in successive years). In this type of repeated measurements, the observations are likely to be auto-correlated and therefore cannot be regarded as a random sample, thus violating the fundamental assumption of ordinary least squares regression of independent observations. To account for this data structure, linear mixed-effects modeling approach with both fixed and random components was used (Fox *et al*., 2001). Since correlation of annual observations for the same plot was very low we decided not to include plot factor in the variance component model. However, the observations for the same year were more cross correlated due to the annually varying conditions. This was accounted for by including the random year factor in the variance component model and by allowing the intercept to vary randomly for each year, this results in a model with random intercept. This structure was used for both the logistic probability of occurrence and conditional yield models. Figure 3 shows the yearly variability of mushroom production.

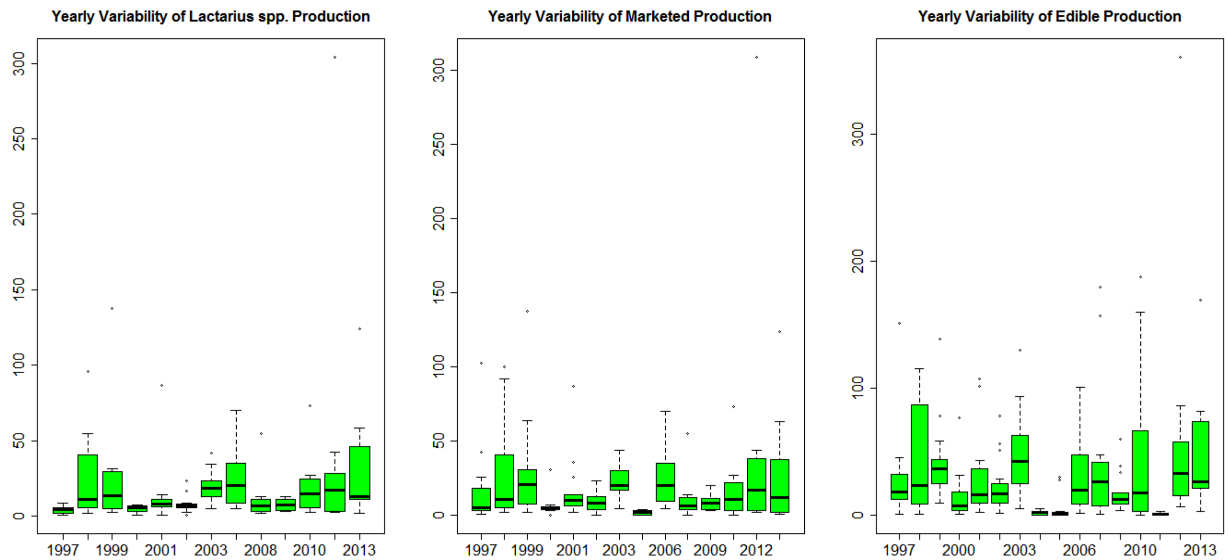

Figure 3. Inter-annual variability in mushroom production (*Lactarius spp*. indicates *L.* group *deliciosus* production)

2.3.1. Mixed-effects logistic regression models

The models for the probability of mushroom occurrence are of the logistic form (Eq. 4) in which the logit of probability of occurrence at plot i (pi) is a linear function of the predictors included (x_k), their beta-coefficients (β_k), year random effect (b_0) and unexplained error (ε) is assumed to follow a binomial distribution (Hosmer and Lemeshow, 2000).

$$\ln\left(pi\middle|\frac{pi}{1-pi}\right) = \beta_o + \beta_1 x_{1i} + \beta_2 x_{2i} + \cdots + \beta_k x_{ki} + b_o + \varepsilon_i \qquad \text{Eq. 4}$$

The predictors (precipitation, temperature, soil and stand variables) were added to the model in a systematic manner to check how much they would improve the previous model. In each category of the predictors the significant predictors and the best model is selected followed by checking how it can be improved by incorporation of variables in the next category of predictors. Different ways of entering the predictor was checked and the results were consistent.

2.3.2. Linear mixed-effects models

All the parameters used for fitting the logistic regression models were used. The models were fitted using linear mixed-effects regression modeling approach. We followed similar pattern for putting the predictors in our model as we did for the logistic regression models.

The basic equation (Eq. 2) for the linear mixed-effect model is specified as the production of mushroom in kg ha^{-1} yr^{-1} in logarithmic scale, conditional on the probability of mushroom occurrence, which is a linear function of the predictors (fixed effects) (x), a random year factor (a_0) and unexplained error (ε).

Since the predicted conditional production is in logarithmic scale it needs to be back transformed. A Snowdon (1991) correction factor was calculated for each model to correct for the back-transformation bias due to the logarithmic transformation of the predicted values.

2.3.3. Model parameterization and evaluation

The lme4 package of R software (R i386 3.0.3) has been used for fitting and analyzing mixed-effect models. The models were parameterized (the values of beta-coefficients in the equations were estimated) using the 'glmer' and 'lmer' functions for the generalized mixed effect models and linear mixed effect models respectively (Bates *et al*., 2014). The 'glmer' uses maximum likelihood (Laplace Approximation), and 'lmer' uses the Restricted Maximum likelihood (REML).

Bayesian Information Criterion (BIC) was used to check trade-off between model parsimony and predictive performance of both nested and non-nested models. BIC assesses the overall fit of a model based on Bayesian comparison of models. Under the assumption that we do not have any prior preference for one model over the other, BIC identifies the model that is more likely to have generated the observed data. The model with smaller BIC is preferred. How much one model is preferred over the other depends on the magnitude of the difference. Presence of multi-coliniarity was also checked by observing their correlation matrix.

The following criteria were considered in model evaluation: a) agreement with current biological knowledge, b) simplicity and robustness, c) statistical significance ($p<0.05$), d) non-biasness, and e) homocedasticity and normal distribution of residuals.

The conformity with statistical assumptions was evaluated and no extreme violations were observed (see appendix 1 for results of checking the assumptions).

3. Results

3.1. Probability of occurrence models

The models selected for predicting the probability of occurrence of edible, marketed and *Lactarius* group *deliciosus* mushrooms are respectively presented in Eq. 5, 6, and 7.

$$\mathbf{Y = ProbEdible = -1.9841 + 0.4741 * P_{autumn/10}} \quad \text{Eq. 5}$$

$$\mathbf{Y = ProbMarketed = -4.0914 + 0.3753 * P_{autumn/10}} \quad \text{Eq. 6}$$

$$\mathbf{Y = ProbLactarius = 1.85737 + 0.2431 * P_{autumn/10} - 0.8845 * pH} \quad \text{Eq. 7}$$

The estimated probability of success, i.e. the probability of mushroom presence at a given plot and year is given by $\mathbf{P = 1/(1 + exp(-Y))}$

The logistic regression analysis showed that autumn precipitation (in millimeters), which is the sum of the total rainfall in the months of August, September and October to be significant predictor in all the three models i.e. the probability of occurrence for edible, marketed and *Lactarius* group *deliciosus* mushrooms. In edible and marketed logistic models no other variable has been observed to be significant other than autumn precipitation. However, pH has been observed to be significant predictor for probability of occurrence of *Lactarius* group *deliciosus*. The models indicate higher autumn precipitation increase the probability of occurrence of the three categories of mushrooms in the modeling. One unit increase in the scaled autumn precipitation is associated with 0.4741 kg ha^{-1} yr^{-1}, 0.3753 kg ha^{-1} yr^{-1}, and 0.2431 kg ha^{-1} yr^{-1} increase in the log odds of presence of edible, marketed and *Lactarius* group *deliciosus* respectively.

Taking the exponent of the log odds (indicated in units odd ratio), gives the Odds Ratio (OR) (Table 4), which shows that a one unit increase in the scaled autumn precipitation increases the odds of presence of edible, marketed and *Lactarius* group *deliciosus* mushrooms in the plots by a multiplicative factor of 1.606, 1.455 and 1.275 respectively or 60.6%, 45.5% and 27.5% respectively. One unit increase in pH decreases the *Lactarius* group *deliciosus* mushroom production by a multiplicative factor of 0.412 or by 58.8%. The increment in percentage of mushroom production would be much higher for more than one unit increase of autumn precipitation (in addition, the values fitted in the model are scaled by division of 10).

Table 4. Coefficients (Estimates), standard error (SE), Wald Z value, p-value, odds ratio (OR) and 95% confidence interval for fixed effect part of the three mixed-effects logistic models.

Model	Predictor	Estimate	Std.Error	Z	Pr(>|Z|)	OR	Conf.int(OR)
Edible	Intercept	-1.9841	2.5920	-0.766	0.4440		
	(P_autumn)/10	0.4741	0.2373	1.998	0.05*	1.606	1.0996 - 3.2793
	AIC= 129.8	logLik =-61.9					
	BIC=140.4	deviance=123.8					
		df.resid=252					
Marketed	Intercept	-4.0914	1.5134	-2.703	0.00686**		
	(P_autumn)/10	0.3753	0.1189	3.156	0.00160 **	1.455	1.1888 -1.9884
	AIC= 252.7	logLik =123.3					
	BIC= 263.3	deviance=246.7					
		df.resid=252					
Lactarius* group *deliciosus	Intercept	1.85737	2.2098	0.840	0.40061	6.4068	
	(P_autumn)/10	0.2431	0.0805	3.019	0.0025**	1.275	1.089 - 1.4932
	pH	-0.8845	0.3312	-2.671	0.00757**	0.412	0.2158 -0.7903
	AIC= 279.8	logLik =-135.9					
	BIC= 293.9	deviance=271.8					
		df.resid= 251					

The variance components accounted by the random year factor in the logistic regression models are 6.731, 2.546, and 2.049 for edible, marketed and *Lactarius* group *deliciosus* mushrooms respectively (Table 5).

Table 5. Variance and standard deviation of the best mixed-effects logistic models for edible, marketed and *Lactarius* group *deliciosus* mushrooms occurrence

Year/ Random effect	Edible	Marketed	Lactarius
Variance	6.731	2.546	2.049
Std.Dev.	2.594	1.596	1.432

Occurrence of mushroom seems to happen starting 100 mm of autumn rainfall in the study area. There is an overlap of the presence and absence of mushroom around the 100 mm of rainfall mark, this may be explained by other stand and soil variables (Figure 4, 5, 6).

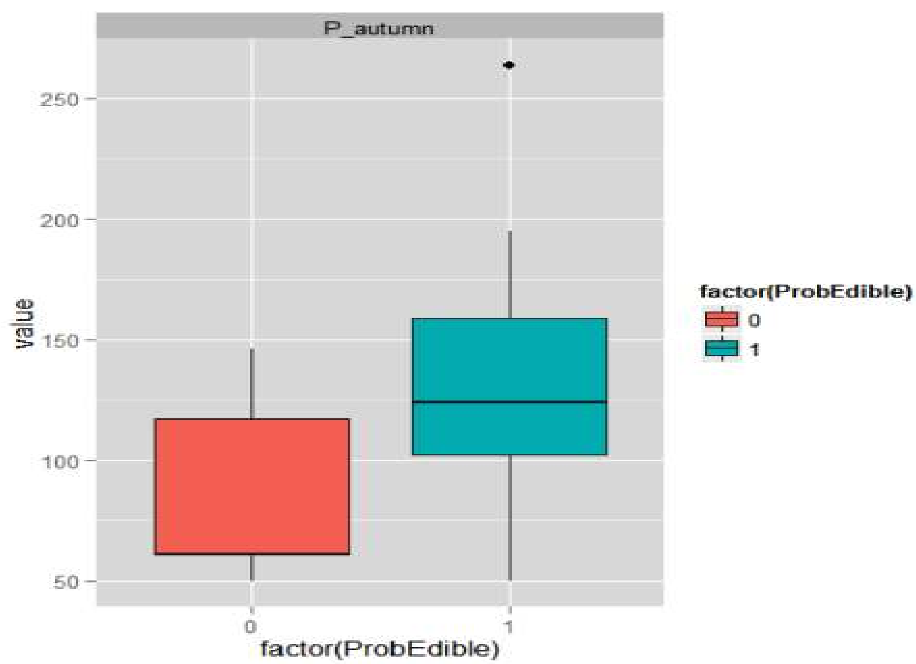

Figure 4. Distribution of autumn precipitation over the probability of occurrence of edible mushrooms

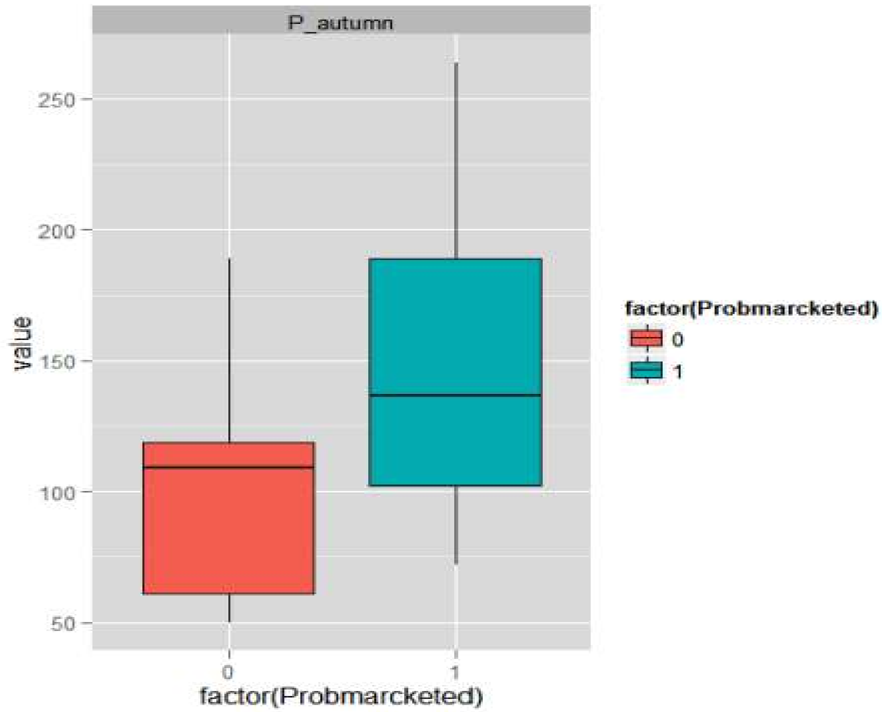

Figure 5. Distribution of autumn precipitation over the probability of occurrence of marketed mushrooms

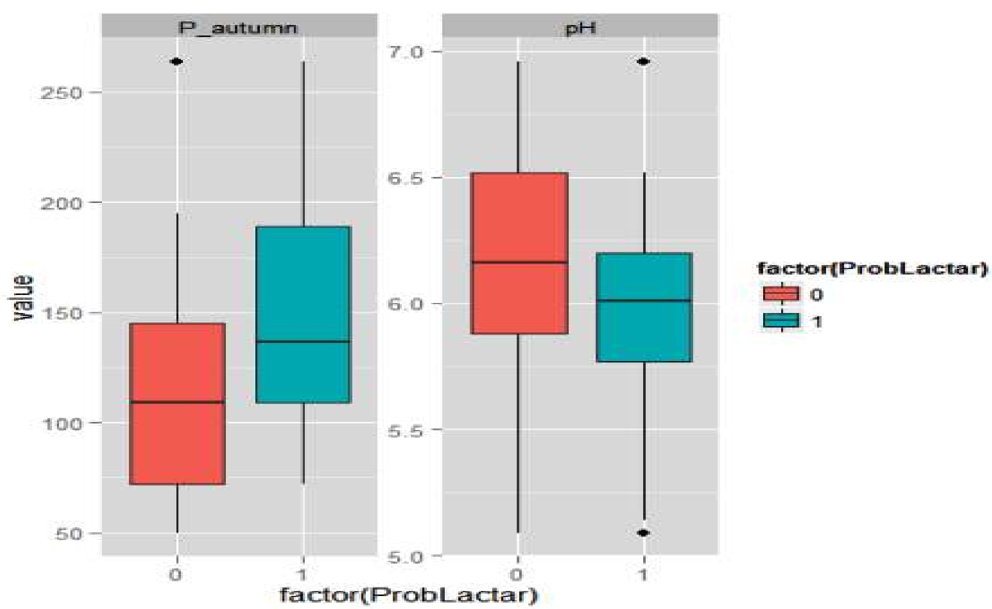

Figure 6. Distribution of autumn precipitation and pH over the probability of occurrence of *Lactarius* group *deliciosus*

3.2. Conditional yield models

43.23% of the total variance of the random effect in the Conditional edible mushroom model is attributed to the year random effect; 20.71% and 13.1% in the Marketed and *Lactarius* group *deliciosu* conditional yield models respectively (Table 6).

Table 6. Measures of variability in mushroom production due to year random effect for the conditional yield models

Model	Random Effect	Variance	Std.Dev
Edible	Year	1.302 **(43.23%)**	1.141
	Residual	1.710	1.308
Marketed	Year	0.3922 **(20.71%)**	0.6262
	Residual	1.5016	1.2254
Lactarius* group *deliciosus	Year	0.1645 **(13.1%)**	0.4056
	Residual	1.0935	1.0457

The models for predicting the conditional yield of edible, marketed and *Lactarius* group *deliciosus* mushroom in each plot (kg of fresh weight) per year are given as:

$$\mathbf{Edible = ln(Y) = 1.11303 + 0.0347 * P\_set}$$

$$\mathbf{Marketed = ln(Y) = 2.6284 - 0.0074 * oldest.tree}$$

$$\mathbf{Lactarius = ln(Y) = 1.2792 + 0.00757 * I(P_{set} + P_{oct}) + 0.53448 * Texture_1 + 0.6919 * Texture_2 - 0.00414 * oldest.tree}$$

Where: P_{set} is total precipitation is the month of September; oldest.tree is the age of the oldest tree in the plot; $I(P_{set} + P_{oct})$ is the sum of the total precipitation in the month of September and October; $Texture_1$ is loamy-sand soil texture; $Texture_2$ is sandy-loam soil texture.

The significant predictor in the conditional edible yield model is only P_{set} and only oldest.tree in the plot for the conditional marketed yield model. In the conditional *Lactarius* group *deliciosus* yield model the significant predictors are $I(P_{set} + P_{oct})$, $Texture_1$, $Texture_2$, and oldest.tree.

One unit increase of P_{set} increases the conditional yield of edible in the logarithmic scale (log scale) by 0.0347, for marketed mushroom one unit increase in the age of the oldest tree decreases the conditional yield in the log scale by 0.0074. One unit increase in $I(P_{set} + P_{oct})$, increases the conditional yield of *Lactarius* group *deliciosus* in the log scale by 0.00757. Change from sandy soil to $Texture_1$ (Loamy sand) and $Texture_2$ (Sandy loam) increases the conditional yield of *Lactarius* group *deliciosus* in the log scale by 0.53448 and 0.6919 respectively. One unit increase in the age of the oldest tree decreases the conditional yield of *Lactarius* group *deliciosus* in log scale by 0.00414 (Table 7).

Table 7. Fixed effect of the selected conditional yield models and Snowdon correction

Model	Predictor	Estimate	SE	t value	Pr(>|t|)	Conf.int(95%)
Edible	Intercept	1.11303	0.59733	1.863	0.0842	-0.0541 - 2.2732
	P_set	0.03471	0.01428	2.431	0.0298 *	0.0069 - 0.0626
	Snowdon Correction	1.804405				
Marketed	Intercept	2.628387	0.24228	10.849	0.00 ***	2.1457 - 3.1035
	Oldest.tree	-0.007357	0.00224	-3.288	0.0013**	-0.0117 - -0.0029
	Snowdon Correction	1.911274				
Lactarius* group *deliciosus	Intercept	1.2792	0.44859	2.852	0.0125*	0.4032 - 2.1297
	$I(P_{set} + P_{oct})$	0.007566	0.00328	2.306	0.05*	0.0013 - 0.0141
	Texture_1	0.534477	0.23574	2.267	0.025*	0.0376 - 0.9798
	Texture_2	0.691881	0.28396	2.437	0.017*	0.1198 - 1.2357
	Oldest.tree	-0.004144	0.00210	-1.974	0.05*	-0.0082- 0.0001
	Snowdon Correction	1.770149				

3.2.1. Performance of the conditional mushroom yield models

The models predictions were rather unbiased after back-transforming the prediction to the original scale and correcting by means of Snowdon's correction factor (Table 7) for the back-transformation bias. The expected relationship between observed and predicted values followed rather well the 1:1 equality line which denotes the perfect fit (Figure 7). Therefore, most of the disagreement between predictions and observations arose from the scatter due to the high unexplained variation of mushroom yield. The conditional model for edible mushroom appears to fit well in the yield ranging 20 to 40 kg ha^{-1} yr^{-1} and over estimates lower yield and under estimates maximum yields. The Conditional model for the marketed mushrooms is observed to fit very well in all the ranges of the production. Similarly the *Lactarius* group *deliciosus* model is very well fit; however, it tends to overestimate maximum yield.

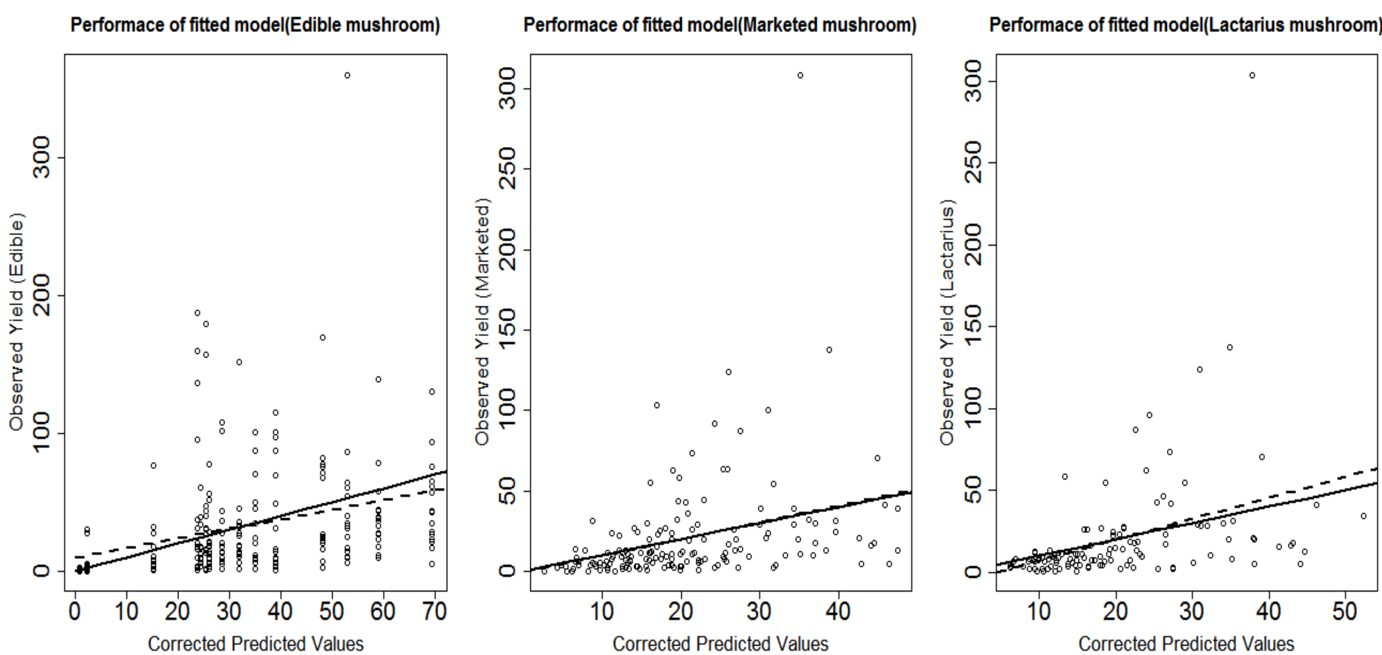

Figure 7. Performance of the selected conditional yield models (The solid line is the line of perfect fit where-as the dashed line indicates the fit of the selected model)

3.2.2. Simulation

Figure 8 shows some simulation tried based on the models. For edible mushroom it has been tried to see the effect of change in September rainfall by fixing the autumn precipitation at mean value. The trend shows an increase in the amount of rainfall in September increases the yield of edible mushroom. At mean value of autumn precipitation, an increase in age of the oldest tree resulted in reduction of marketed mushroom yield. Keeping the values of autumn precipitation, pH at mean and age of oldest tree at mean, minimum and maximum values and in sandy loam soil texture class, the increase in the total rainfall in October and September increased the yield of *Lactarius* group *deliciosus*. These trends indicate the distribution of the rainfall in addition to its amount is an important factor in the yield of mushrooms. Autumn precipitation is significant factor for the occurrence of mushrooms; however, the simulation produced by keeping the autumn precipitation at mean value and changing the amount of September precipitation in case of edible mushroom and total rainfall in September and October for *Lactarius* group *deliciosus* indicated that the way the precipitation is distributed also matters. The simulation by fixing the autumn precipitation at maximum and minimum recorded values still showed similar trend with the one at mean value.

The effect of total rainfall in September and October at different age of oldest tree was simulated by fixing the age at mean (solid line), minimum (dashed line) and maximum (dotted line) values (Figure 8). The effect of rainfall was observed to be higher in plots with the lowest age and least in highest age (Figure 8).

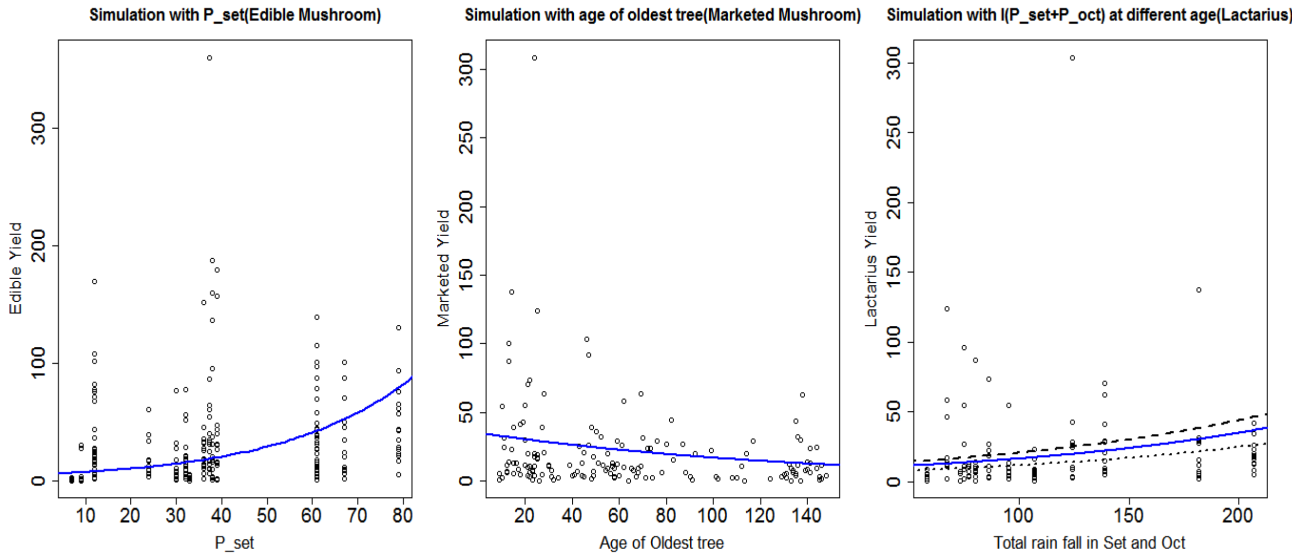

Figure 8. Simulation of edible, marketed and *Lactarius* group *deliciosus* mushrooms (in sub-figure for *Lactarius*, solid line is the simulation at mean age, dashed and the dotted line represent, respectively, the simulation at the minimum and maximum stand age recorded in the modeling data).

4. Discussion

Our results show the influence of rainfall (especially autumn rainfall) as a driving factor for the occurrence of edible, marketed and *Lactarius* group *deliciosus* considered in this study. It has also been observed that stand and soil characteristics become important predictors as we narrow down from broad category like edible to level of *Lactarius* group *deliciosus*. This suggests that considering at a genus or species level may reveal important relationships involved in the occurrence and growth of the mushroom being investigated. Previous studies have also indicated that the emergence of sporocarps is strongly related to weather conditions specially rainfall (Bonet *et al*., 2004; Martínez-Peña *et al*., 2012a). Temperature is another important variable for mushroom yield; however, none of the temperature variables were significant at $p<0.05$ values in our study. This may be because the year random factor considered may account for some of the between-year variation in temperature. In a climate change scenario where an increase in temperature is considered, its consequent effect on transpiration and surface evaporation would inevitably affect both occurrence and yield of mushroom.

Our result has indicated that increasing the age of oldest tree (i.e. a proxy for stand age) decreases the production of both marketed and *Lactarius* group *deliciosus*. This is in line with the study of Fernandez-Toiran *et al*. (2006), where higher abundance of *Laccaria laccata* and *L. deliciosus* was found in the age class of 11-20 as compared to the oldest age class. This might indicate that marketed mushroom production could be enhanced by maintaining rather young stands. In this way, Bonet *et al*. (2012) has reported positive effect of thinning on *Lactarius* group *deliciosus* production in 50 years old *P. pinaster* forests; hence, thinning activity to maintain young stands could play a role to maximize the production of these mushrooms.

Ágreda *et al*. (2013) also indicated that *L. deliciosus* sporocarp production is highly influenced by *Pinus pinaster* stand age class and maximum production was reported to occur in the age class of 11-20. Bonet *et al*. (2010) also found less sporocarp biomass in old-growth stands than in younger stands. However, Bonet *et al*. (2004) found no significant difference in fresh weight yield of *L*. group *deliciosus* in *Pinus sylvestris* stands with different stand age. In our study, the slope and aspect of the sampling plots were quite homogeneous; however, Bonet *et al*. (2008) observed that the production of marketed *Lactarius* was related to aspect, slope and also stand basal area which is not considered in our modeling data. It has been observed that in *Pinus pinaster,* young trees start the growing season earlier than old trees (Viera *et al*., 2009). This may possibly give advantage to *Lactarius* group *delicious* in young stand ages to get more photosynthate from the photosyntheticaly active younger trees and enhance their growth.

It has also been reported that in older stand age classes *L. deliciosus* registered a recovery in production (Ágreda, 2013; Martínez-Peña *et al*., 2012b). Even though there is a decrease in the production of marketed and *Lactarius* group *deliciosus*, the trend in our study shows as there seems to be a slight recovery in the highest oldest tree age (Figure 9).

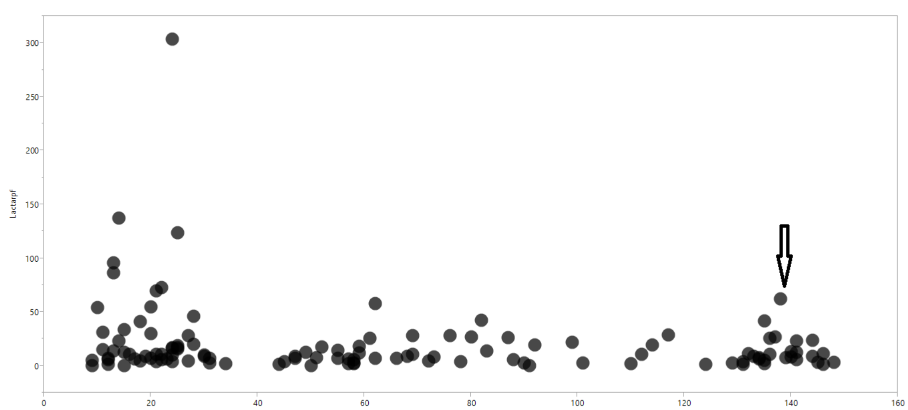

Figure 9. Relationship between stand age and *Lactarius* group *deliciosus* yield. The data suggests a slight recovery of mushroom yield in plots corresponding to the highest stand age class (concentration of the dots increase at age >120)

Our result showed significant effect of pH and soil texture specifically in *Lactarius* group *deliciosus.* In *Pinus sylvestris* forests, Martínez-Peña *et al*. (2012a) reported that none of the soil variables they used like pH, texture, water retention capacity were significant in the modeling; however, they have indicated a strong correlation with mushroom yield (including with yield of *L.* group *deliciosus*). They have mentioned negative correlation of sand content with *Lactarius* yield, where as silt and clay content were positively correlated which is in line with our result. This could be due to the fact that sandy soils have a lower water holding capacity, and the rainfall cannot be utilized efficiently in such soil type. In addition, as the area is characterized by higher summer drought, water holding capacity of the soil could be very critical. In their study pH was not correlated with *Lactarius* but negatively correlated with *Boletus edulis*. However, our result showed a negative relationship between pH and occurrence of *L.* group *deliciosus*. The genus *Lactarius* has been reported as being only slightly affected by variations in pH (Espigol, 1999). However, other results also indicated better performance in the acidic range. Barros *et al*. (2006) showed that the growth of *Lactarius deliciosus* mycelium is significantly better in the slightly acidic soil (pH=5) but the effect of pH was dependent on the medium they used. In a study conducted in two commercial nurseries a higher percentage of colonization was observed for *Lactarius* genus on more acidic soil (pH=4.5-5.5) (Gonzalez-Ochoa *et al*., 2003).

Madeira and Ribeiro (1995) indicated that decomposition of *P. pinaster* needles increase the pH values. In line with this Kurz *et al.* (2000) indicated decomposition rate of *Pinus pinaster* needles reaches 50% loss of mass after 5.1 years; hence, the more decomposition of the needles in older stands could results in an increase of the pH. This could also justify the negative effect of increasing both stand age and pH which could be related due to the expected high decomposition of the needles in older stands. It has been indicated as there is a shortage of information regarding the soil requirements of many mushrooms, hence; this result can be a highlight for making further structured study.

The simulation emphasizes the importance of not only amount of rainfall but also its distribution on mushroom production. In addition it has revealed that increasing amount of rainfall would have more positive impact in younger stand ages.

The models provided in this study are valuable tools that can be used to predict the occurrence as well as quantify the yield given the occurrence of mushroom for edible, marketed and *L.* group *deliciosus* in *P. pinaster* forests in Central Spain. In line with this study an article recently published aims at predicting the spatial distribution of *Lactarius deliciosus* and *Lactarius salmonicolor* in Turkey using logistic regression models (Mumcu Kucuker and Baskent, 2014). This kind of approach is useful to have prediction models that predict the occurrence and distribution of the mushrooms. We underline the need for further research accounting for different stand characteristics, to better understand their relationship with mushroom occurrence and productivity and could provide a concrete recommendation for forest managers. But still these models could provide tentative recommendations. In addition they can be helpful for mushroom pickers in the area, and may also be of use to facilitate the tourism linked to mushroom picking. The models are climate sensitive with respect to change in precipitation and could be useful for making predictions under climate change conditions.

5. Conclusions

With the current trend towards integrated forest management and the increased economic value of mushrooms this study shades light on the factors that affect mushroom production and provides a tool (i.e. models) to predict the occurrence and possibly quantify the amount of production and could be of use.

The two-stage modeling approach has enabled us to assess the effect of the climatic, soil and stand variables on mushroom production by separately modeling the probability of occurrence and yield given the presence. This approach has created a room to learn more about the system than if we used a single model for the yield. Moreover, we have been able to combine the results from the two analyses to provide predictions that would be helpful for mushroom picking and also for managers. We recommend this kind of modeling approach for handling data from a phenomenon with possibility of zero values, in our case mushroom production data. This kind of approach is useful to have prediction models that predict the occurrence and spatial distribution of the mushrooms and their yield given the occurrence.

Further research by incorporating various stand variables like stand basal area would be worthwhile to improve the models and also to better incorporate it with forest management.

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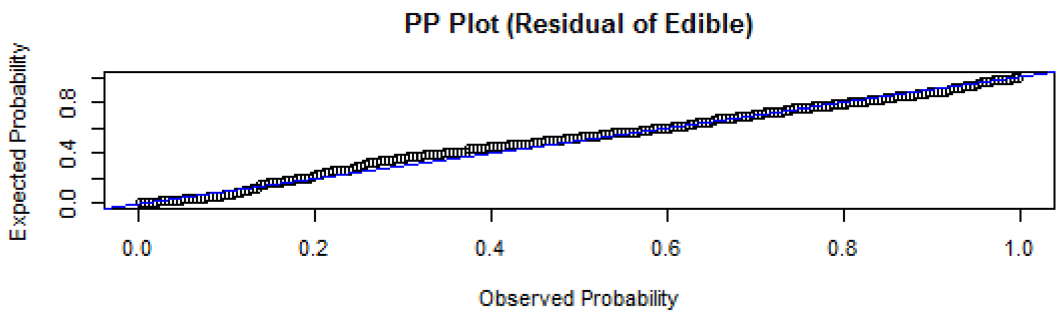
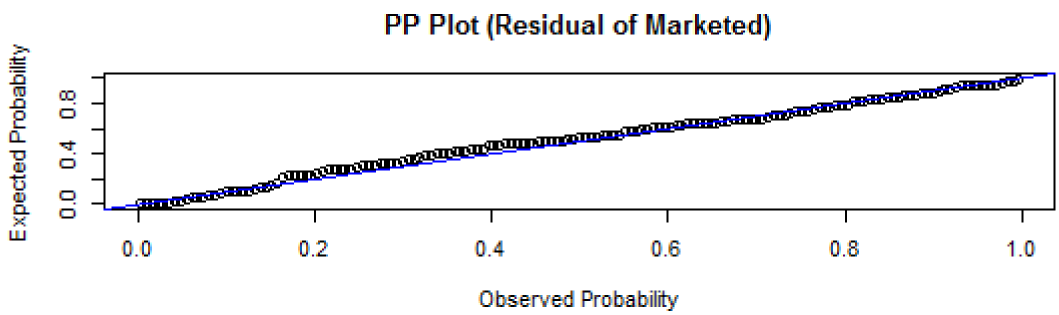
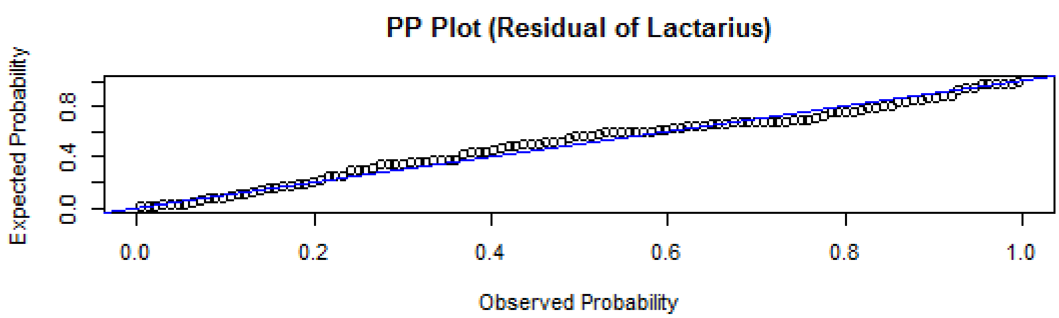
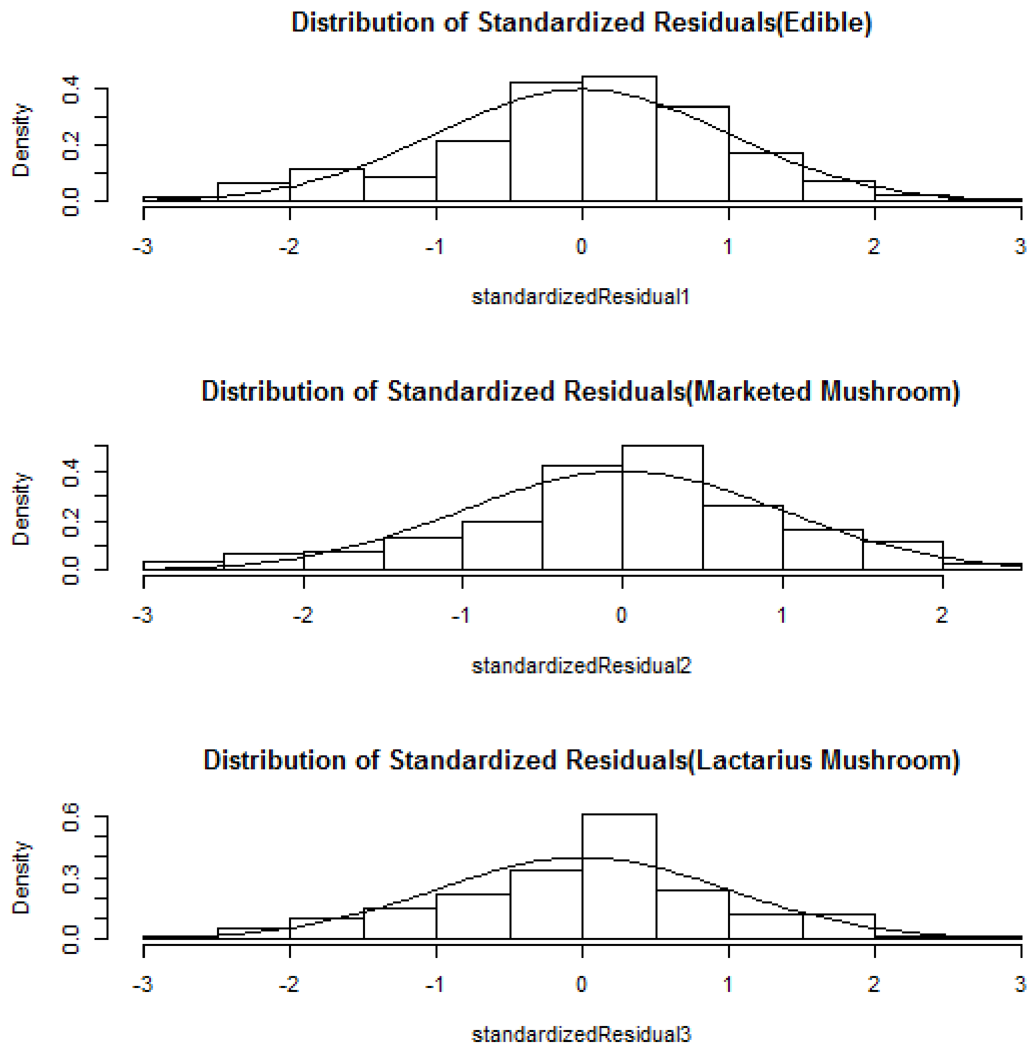
Appendix I: Checking statistical assumptions



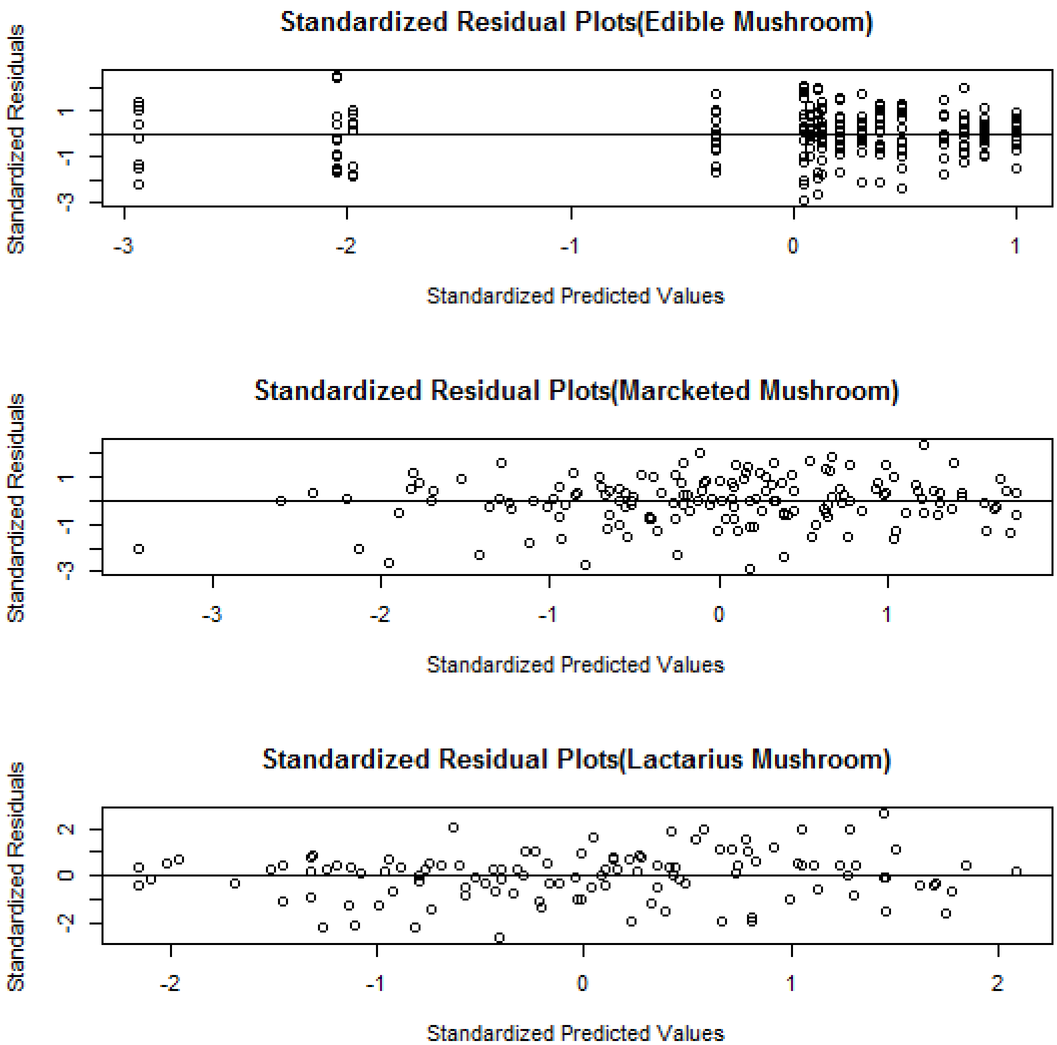




Slide1. Test for the assumption that the residuals are normally distributed. The distribution is considered to be normal to the extent that the plotted points match the diagonal line.



Slide2. Test for the assumption that the residuals are normally distributed. To the extent the histograms matches the normal distribution, the residuals are normally distributed.



Slide3. Test for homogeneity of variance (homoscedasticity) assumption. The homogeneity of variance assumption is supported to the extent that the vertical scatter is the same across all x values. It is also to assess the assumption that the variables have a linear relationship. The linearity assumption is supported to the extent the amount of points scattered above and below the line is equal.