Modelling the production and species richness of wild mushrooms in pine forests of the Central Pyrenees in northeastern Spain

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Abstract: Multiple-use forestry requires comprehensive planning to maximize the utilization and sustainability of many forest resources whose growth and productivity are interconnected. Forest fungi represent an economically important non-wood forest resource that provides food, medicine, and recreation worldwide. A vast majority of edible and marketed forest mushrooms belong to fungi that grow symbiotically with forest trees. To respond to the need for planning tools for multiple-use forestry, we developed empirical models for predicting the production of wild mushrooms in pine forests in the South-Central Pyrenees using forest stand and site characteristics as predictors. Mushroom production and species richness data from 45 plots were used. A mixed modelling technique was used to account for between-plot and between-year variation in the mushroom production data. The most significant stand structure variable for predicting mushroom yield was stand basal area. The stand basal area associated with maximum mushroom productivity (15–20 $m^2 \cdot ha^{-1}$) coincides with the peak of annual basal area increment in these pine forests. Other important predictors were slope, elevation, aspect, and autumn rainfall. The models are aimed at supporting forest management decisions and forecasting mushroom yields in forest planning.

Résumé : La foresterie à usages multiples requiert une planification détaillée pour maximiser l'utilisation et la durabilité des nombreuses ressources forestières dont la croissance et la productivité sont interconnectées. Les champignons forestiers constituent une ressource forestière non ligneuse économiquement importante qui fournit de la nourriture, des médicaments et des activités récréatives partout dans le monde. La vaste majorité des champignons forestiers comestibles qui sont mis en marché appartiennent aux champignons qui croissent en symbiose avec les arbres forestiers. Dans le but de répondre au besoin en outils de planification pour la foresterie à usages multiples, nous avons développé des modèles empiriques pour prédire la production de champignons sauvages dans les forêts de pin dans la partie sud des Pyrénées centrales en utilisant les caractéristiques de la station et du peuplement forestier comme prédicteurs. Des données de production et de richesse en espèces de champignons provenant de 45 parcelles ont été utilisées. Une technique de modélisation mixte a été utilisée pour tenir compte de la variation entre les parcelles et entre les années dans les données de production de champignons. La variable de structure du peuplement la plus significative pour prédire la production de champignons était la surface terrière. La surface terrière du peuplement associée à la productivité maximale de champignons (15–20 $m^2 \cdot ha^{-1}$) coïncide avec le pic d'accroissement annuel de la surface terrière dans ces forêts de pin. Les autres prédicteurs importants étaient la pente, l'altitude, l'exposition et la précipitation automnale. Les modèles visent à supporter les décisions d'aménagement forestier et à prédire les rendements en champignons dans la planification forestière.

[Traduit par la Rédaction]

Introduction

Forest planning has historically focused on timber and wood production, but changes in the globalization of the wood market as well as public concerns for ecosystem protection and recreational demands have increased the relative importance of other products and services in many forests. Nonwood forest products, collection of berries, edible mushrooms, medicinal plants, and floral greens, provide important recreational and commercial activities in the rural forested areas of the world (Food and Agriculture Organization of the United Nations 1995) and require comprehensive approaches for sustainable utilization (Cocksedge 2006). Edible and medicinal wild forest fungi are among the most

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valuable nonwood forest products. Forest fungi provide income annually for mushroom hunters as opposed to the periodic income from timber sales. The relative importance of income derived from fungi, as compared with timber production, depends on the forest tree species, site quality, and the market value of the mushroom species found on site (Alexander et al. 2002).

Annual mushroom production varies considerably in response to weather conditions, most notably timing and quantity of rainfall (O'Dell et al. 1999; Bonet et al. 2004). Inventories carried out over several years provide reliable baseline data for estimating both fungal diversity and fungal production (Martínez de Aragón et al. 2007). Repeated mushroom inventories allow managers to monitor the response of the mycological resources to silvicultural interventions (Pilz and Molina 2002).

In the Spanish Pyrenees, the low profitability of timber production has decreased investments in forest management with a consequent loss of income from timber sales (Mogas et al. 2005). This is creating a serious downward spiral, since revenues are not sufficient to support even the most basic activities such as road maintenance and fire prevention. Nonwood forest products, and especially mushrooms, are key products that can break this spiral by providing additional income that can make forestry profitable. Additionally, mushroom picking has become an increasingly popular recreation activity in the autumn season and has been recognized by Catalans as one of the most valuable recreational activities in the forest (Mogas et al. 2006).

What are the most important mushrooms found in these forests? The majority of the edible and large fleshy fungi are the fruitbodies of ectomycorrhizal fungi that grow in symbiosis with forest trees. Studies conducted in the South-Central Pyrenees have characterized the mushroom production of ectomycorrhizal forest fungi (EMF) associated with different tree species. Bonet et al. (2004) reported yields of 60.6 kg·ha^{-1}·year^{-1} in Scots pine (Pinus sylvestris L.) plantations. Martínez de Aragón et al. (2007) measured a mean productivity of 29.4 kg·ha^{-1}·year^{-1} in natural P. sylvestris, European black pine (Pinus nigra Arnold), and Aleppo pine (Pinus halepensis P. Mill.) forests.

Empirical predictive models for mushroom production incorporating silvicultural parameters are helpful for multiple-use forest managers because they are compatible with existing management planning systems. Recently, Bonet et al. (2008) developed a mushroom yield model for planted P. sylvestris forests that showed that mushroom production was greatest when stand basal area (BA) was approximately 20 m^2·ha^{-1}. Elevation, slope, and aspect were also significant predictors of mushroom production. This first attempt to incorporate mushroom yields into silvicultural models revealed, on one hand, that modelling of wild mushroom yields is possible but, on the other hand, that there is a need to refine and expand the studies in this field. The models of Bonet et al. (2008) are for one species only, and they are for plantations, which are rare in the South-Central Pyrenees.

To better serve forest management and planning, models should be developed for naturally regenerated stands and for a higher number of species.

The aim of the present study was to develop empirical models for predicting the production and species richness of wild mushrooms in planted and naturally regenerated P. sylvestris stands as well as naturally regenerated P. nigra and P. halepensis forests in the South-Central Pyrenees. These pines are the dominant tree species in this region. Data on mushroom production from 45 plots were used. A mixed modelling technique was used to account for between-plot and between-year variation in the mushroom production data. The models are aimed at supporting forest management decisions and forecasting mushroom yields in forest planning.

Methods

Mushroom yield assessments

Mushroom yields were assessed in two sets of plots inventoried in previous studies (see Bonet et al. 2004; Martínez de Aragón et al. 2007). The first set of 24 plots was placed in pure P. sylvestris plantations established in the early 20th century in the counties of Ribagorça (Huesca), Spain, and Alta Ribagorça (Lleida), Spain. These plantations ranged in elevation from 900 to 1500 m with a shrub layer dominated mainly by Buxus sempervirens. Stand age of these plots ranges from 5 to 84 years. Mushroom production and species richness were inventoried in 1995–1997 (Bonet et al. 2004).

The second set of 21 plots was placed in natural P. sylvestris, P. nigra, and P. halepensis forests in the county of Solsonès (Lleida), Spain. The plots were randomly distributed throughout the county in numbers proportional to the area occupied by each tree species, with 11 plots of P. nigra, six plots of P. sylvestris, and four plots of P. halepensis. Stand age of these plots ranges from 23 to 88 years and elevation ranges from 500 to 1500 m. Mushroom production and species richness were inventoried in 1997–2001 and again in 2007 (Martínez de Aragón et al. 2007).

A similar procedure for sampling mushrooms was used for the two sets of data. The plots were monitored at 1-week intervals during the autumn fruiting season (September–December). Data from spring fruiting have not been included due to very low production during spring. Mushroom collection included all epigeous ectomycorrhizal species as well as nonectomycorrhizal edible species (see supplementary table[2]). All sporocarps collected were identified at the species level whenever possible with the help of appropriate mycological keys. Some samples could only be identified to the genus, subgenus, section, or subsection levels. Sporocarp production data are reported as kilograms fresh weight per hectare and are classified by edibility and by marketability. Additional information on the sampling sites, fungal species lists, and sampling methodology can be found in Bonet et al. (2004) and Martínez de Aragón et al. (2007).

Forest inventories

The 45 mushroom plots were inventoried to obtain information on forest stand characteristics in the autumn of 2006 (for the first set of plots) and winter of 2007 (for the second set). The area of the plot on which the trees were measured varied between 0.0314 and 0.102 ha. The mean plot area was 0.057 ha. These plots were established so that at least 100 trees with diameter at 1.3 m (diameter at breast height) >7.5 cm were within the plot. For each plot, diameter at breast height and the radial growth for the last 10 years were measured for all trees. In addition, tree heights, tree ages, and bark thicknesses were recorded for a sample of at least 20 trees per plot.

Stand characteristics during the period 1995–2001 were calculated by subtracting the required number of annual growths from the current tree diameter, assuming that the annual radial growth of a tree was 0.1 times the measured 10-year radial growth. Tree height and age were calculated with plot-specific models, which were fitted using the same tree measurements.

The tree variables obtained from these calculations for different years were used to calculate the following stand-level variables for each year of mushroom inventory: stand BA, number of trees per hectare, mean tree age, mean tree diameter, mean tree height, and standard deviation of diameter and height. The site index of each plot was calculated from the model of Palahí et al. (2004). In addition to growing stock variables, some topographical variables (elevation, slope, and aspect) were included as potential predictors of the mushroom production models.

Modelling

Modelling mushroom production

The modelling data were characterized by multiple measurements for each individual sampling unit (several observations for the same plot) and several sampling units (plots) measured in the same year. In this type of repeated measures data, the observations 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, a multilevel linear mixed model approach with both fixed and random components was used (Fox et al. 2001). Annual observations for the same plot were correlated, which was accounted for by including the random plot factor (or effect) in the variance component model and by allowing the intercept to vary randomly at the plot level (e.g., Searle et al. 1992). Observations for the same year were cross-correlated due to annually varying conditions. Therefore, the random year factor was also used as a variance component in the mushroom production model. The predicted variable in the mushroom production model was the logarithmic transformation of the annual production. This resulted in a linear relationship between the dependent and independent variables and enabled the development of multiplicative production models.

Variables representing forest stand (stand age, BA, number of trees per hectare, dominant tree species, etc.) and site characteristics (site index, slope, aspect, and elevation) were tested as potential fixed predictors, since they may affect both (i) photosynthesis and tree growth and, therefore, the carbohydrates or metabolites transferred to the fungi to support fruiting and (ii) the microenvironment and, therefore, fruiting conditions. Differences in site and forest canopy affect the humidity and temperature of the forest floor as well as the physical and chemical conditions of the soil.

The models were estimated using the MIXED procedure of the computer software SAS/STAT (SAS Institute Inc. 2000–2004). The following was the basic mixed linear model:

$$[1] \quad \ln(y_{ij}) = f(x_1; x_2; ....; x_n) + u_i + u_j + \varepsilon_{ij}$$

where y_{ij} is the mushroom production of plot i in year j (kg·ha^{-1}·year^{-1}), $f(\cdot)$ is the fixed part of the model, x_1, ..., x_n are fixed predictors, u_i is the random plot factor, u_j is the random year factor, and ε_{ij} is the residual (that part of the production that is not explained by the fixed part and random factors). All random components (u_i, u_j, and ε_{ij}) were assumed to be normally distributed with mean equal to zero. The model was fitted for total production, production of edible species, and production of marketed species.

Some potential fixed predictors that were thought to partially explain mushroom yield including dominant tree species, slope, and regeneration method (plantation versus naturally regenerated forest) appeared to be nonsignificant ($p > 0.05$) in the mixed model. However, some of these predictors were significantly correlated with the plot factors, which were solved for the estimated mushroom production models (eq. 1). The predicted random factors are the empirical best linear unbiased predictors, and they can be used for comparing the random factors of different experimental units (for more details see, SAS Institute Inc. 2000–2004). Therefore, models for plot factor were developed based on stand and site characteristics not present in the mixed model (eq. 1). The year factor was also modelled using variables representing weather information (mainly autumn rainfall information) of the measured years, as they are known to be relevant factors in explaining mushroom fruiting and production (Fig. 1).

The models for predicting the plot and year factor were developed using the ordinary least squares technique in SPSS (SPSS Inc. 2005):

$$[2] \quad \begin{aligned} u_i &= f(x_1; x_2; ....; x_n) + \varepsilon_i \\ u_j &= f(x_1; x_2; ....; x_n) + \varepsilon_j \end{aligned}$$

where u_i and u_j are, respectively, the random plot and year factor of the mixed linear model (eq. 1), x_1, ..., x_n are fixed predictors, and ε_i and ε_j are residuals. These models can be used for calibrating the fixed effect model, allowing for the incorporation of predicted plot and year factor in simulations.

Modelling mushroom species richness

In the mushroom species richness data, the dependent variable was distributed as count data, i.e., the data were assumed to have a Poisson distribution. As a result, the number of mushroom species was modelled by using a generalized linear mixed model (GLMM) with a Poisson response (log-link function) (McCullagh and Nelder 1989). The GLMM was estimated using the NLMIXED procedure of the computer software SAS/STAT (SAS Institute Inc.

Fig. 1. Predicted year factors (bars) versus autumn rainfall (squares) calculated as the sum of rainfall in the months of August, September, October, and November.
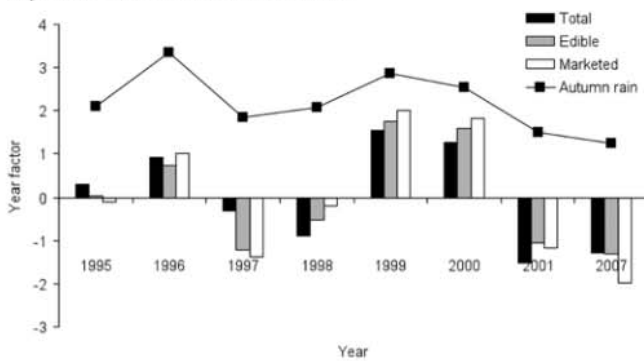
2000–2004). Similarly as in mushroom yield modelling, between-plot differences were taken into account by including the random plot factor in the model. Because in the NLMIXED procedure, only one kind of random factors can be defined, e.g., random plot factors or random year factors, between-year differences were taken into account by including fixed year factors in the mushroom species richness model.

The following was the basic GLMM:

$$[3] \quad y_{ij} \sim \text{Poisson}(p_{ij})$$
$$\ln(p_{ij}) \quad f(x_1; x_2; ....; x_n) + u_i$$

where y_{ij} is the number of mushroom species within 100 m^2 plot i in year j, the conditional distribution of y, given the expected value, p, was Poisson distributed, $\ln(p)$ is a log-link function, $f(\cdot)$ is the fixed part of the model, x_1, ..., x_n are fixed predictors, and u_i is the random plot factor (normally distributed with mean equal to zero). The year factors were included as fixed dummy variables so that the first year 1995 was used as the reference year. The random plot factors were assumed to account for overdispersion (i.e., unobserved heterogeneity) that occurred in the data, since the observed variance (26.2) was clearly larger than the mean number of mushroom species (6.6) (Table 1).

Some of the nonsignificant fixed predictors for number of mushroom species were significantly correlated with the random plot factors solved for the estimated mushroom species richness model (eq. 3). Therefore, models for the plot factor were developed similarly as in mushroom production modelling.

Results

Models for mushroom production

The most significant stand structure variable for predicting mushroom yield was stand BA. The regression analysis showed that two transformations of stand BA (G), namely $\ln(G)$ and H G, were significant predictors. Together, these transformations described the ascending–descending pattern of the relationship between stand BA and mushroom production seen in the data. The effects of site on mushroom yield were best explained by the transformation of three geotopographical variables, elevation, slope, and aspect,

which are known to affect moisture, temperature, light, and other chemical and physical conditions of the site. A variable combining the effects of slope (percent) and aspect (radians), $\ln(\text{Slo} + 1) \times \cos(\text{Asp})$, explained the increasing effect of aspect with increasing slope. This variable had already been used by Stage (1976) to explain the combined effect of aspect and slope on tree growth. However, this predictor did not account for the effect of slope alone on mushroom yield. The logarithmic transformation of elevation (metres), $\ln(\text{Ele})$, explained the positive effect of elevation on mushroom production. No other variables had a significant contribution to the fitting statistics after these variables had been included in the models. The above combination of variables produced the smallest Akaike information criterion (Burham and Anderson 2002). The final model to describe the dependence of mushroom production on stand and site variables was as follows:

$$[4] \quad \ln(y_{ij}) \quad b_0 + b_1 \times \ln(G_{ij}) + b_2 \times \frac{p}{G_{ij}}$$
$$+ b_3 \times \ln(\text{Ele}_i) + b_4 \times \ln(\text{Slo}_i + 1)$$
$$\times \cos(\text{Asp}_i) + u_i + u_j + 3_{ij}$$

where y_{ij} is the mushroom production of plot i in year j (kg·ha^{-1}·year^{-1}), G is stand BA (m^2·ha^{-1}), Asp is aspect (rad), Slo is slope (%, i.e., 458 is equal to 100%), Ele is elevation (m above sea level), u_i is the random plot factor, u_j is the random year factor, and 3_{ij} is the residual. The parameter estimates and variances of the random factors are given in Table 2 together with some fitting statistics. The p values were less than 0.05 for all regression coefficients except for the coefficient of $\ln(\text{Slo} + 1) \times \cos(\text{Asp})$ in the model for marketed mushrooms for which p was 0.0987.

The random plot factor was best explained by slope, dominant tree species of the stand, and, for P. sylvestris, whether the stand was naturally regenerated or planted. The ordinary least squares model for the plot factor was as follows:

$$[5] \quad b_i \quad b_0 + b_1 \times \text{planted}_i + b_2 \times \text{Slo}_i^{1:5}$$
$$+ b_3 \times \text{sylvestris}_i + 3_i$$

where b_i is the plot factor predicted for plot i (see eq. 1), "planted" is a dummy variable that is equal to 1 for planted P. sylvestris stands and otherwise zero, Slo is slope (%), "sylvestris" is a dummy variable equal to 1 for P. sylvestris dominated stands and is zero for P. nigra and P. halepensis dominated stands, and 3_i is the residual.

The random year factor was best explained by the mean autumn rainfall of the region (i.e., the total precipitation during August, September, October, and November). The ordinary least squares model to describe the dependence of year factor on weather data was as follows:

$$[6] \quad b_j \quad b_0 + b_1 \times \ln(\text{AutumnRain}_j) + 3_j$$

where b_j is the year factor predicted for year j (see eq. 1), "AutumnRain" is the total autumn rainfall (mm) during August, September, October, and November in year j, and 3_j is the residual. The parameter estimates and fitting statistics for the plot and year factor models are given in Table 3. All of the regression coefficients of predictors were significant (p < 0.05).

According to the yield and plot factor models, mushroom

Table 1. Summary of the average stand variables, mushroom production, and species richness data for the 45 plots used in modelling.

Variable	Mean	SD	Minimum	Maximum
Stand variable				
T (years)	39.6	14.9	10.4	83.8
H_{dom} (m)	12.1	3.7	3.3	21.0
G ($m^2 \cdot ha^{-1}$)	21.8	10.3	1.0	57.0
N_{trees} (ha^{-1})	1558.7	594.0	717	3056
D_m (cm)	17.6	5.5	4.9	34.9
SI (m)	21.3	3.1	13.3	27.5
Elevation (m)	1049.0	311.2	530.0	1528.0
Aspect (8)	189.1	114.6	4.0	356
Slope (%)	21.7	8.6	5.0	38
Mushroom production and species richness				
Total ($kg \cdot ha^{-1} \cdot year^{-1}$)	68.7	116.2	0.0	743.5
Edible ($kg \cdot ha^{-1} \cdot year^{-1}$)	40.0	66.6	0.0	416.4
Marketed ($kg \cdot ha^{-1} \cdot year^{-1}$)	16.7	33.0	0.0	211.7
No. of species (100 $m^{-2} \cdot year^{-1}$)	6.6	5.1	0	22

Note: T, stand age; H_{dom}, dominant height; G, stand basal area; N_{trees}, the number of trees per hectare; D_m, mean diameter; SI, site index at a reference age of 100 years.

Table 2. Parameter estimates and variances of random factors, fitting statistics, and the Snowdon correction factors for mushroom production (eq. 4) and mushroom species richness (eq. 7) models.

	Total production (eq. 4)	Edible mushrooms (eq. 4)	Marketed mushrooms (eq. 4)	No. of species (eq. 7)
Parameter (and predictor)				
b_0 (constant)	−23.960	−26.232	−28.362	−8.055
b_1 (lnG)	4.590	4.274	2.635	1.703
b_2 (H G)	−2.375	−2.376	−1.338	−0.768
b_3 (ln Ele)	3.441	3.824	3.956	1.197
b_4 (ln(Slo + 1) × cos(Asp))	0.445	0.435	0.219	0.127
Variance components				
s^2_{plot}	0.733	0.625	1.882	0.174
s^2_{year}	1.389	1.534	2.179	0.074
$s^2_{residual}$	3.782	4.705	4.464	
Total variance	5.905	6.864	8.525	
−2 × log-likelihood	869.9	905.6	923.0	1036.2
AIC	885.9	921.6	939.0	1062.2
Snowdon correction	1.972	1.917	4.665	1.054
Snowdon correction with predicted plot factor	1.947	1.926	3.915	1.033
Snowdon correction with predicted plot and year factors	1.038	1.015	1.694	

Note: Low values of residual variance, −2 × log-likelihood, and Akaike's information index (AIC) imply good fit.

productions are the highest when stand BA is 10 to 20 $m^2 \cdot ha^{-1}$ (Fig. 2). Elevation and aspect also strongly affect the predicted mushroom production. When elevation increases from the lowest (500 m) to the highest (1500 m), mushroom productivity increases by more than 10 times (Fig. 3). A similar positive trend is seen when aspect changes from south to north (Fig. 3). Slope, which is a predictor in the plot factor models, also had a very clear effect on mushroom yield (see Fig. 3). The steeper the slopes, the lower were the mushroom yields.

Pinus sylvestris dominated stands produce higher (more than double) mushroom yields than P. nigra or P. halepensis dominated stands. In addition, mushroom yields were greater in naturally regenerated P. sylvestris stands than in planted P. sylvestris stands (Fig. 4).

When the mushroom yield model is used together with the plot and year factor models, it is possible to see the effect of total autumn rainfall on the production of mushrooms. The models predict five times greater mushroom yields when autumn rainfall is doubled (Fig. 5).

Table 3. Parameter estimates and fitting statistics for the plot and year factor models.

Parameter (and predictor)	Total production (eq. 5)	Edible production (eq. 5)	Marketed production (eq. 5)	No. of species (eq. 8)
Plot factor model				
b_0 (constant)	0.101	0.115	0.275	0.113
b_1 (planted)	−0.473	−0.405	−0.985	−0.00262
b_2 ($Slo^{1.5}$)	−0.004	−0.003	−0.008	0.271
b_3 (sylvestris)	0.863	0.662	1.628	
R^2	0.239	0.214	0.243	0.168
$s^2_{residual}$	0.266	0.188	0.961	0.120
Year factor model				
b_0 (constant)	−16.833	−16.854	−21.490	−3.587
b_1 (AutumnRain)	3.151	3.155	4.025	0.670
R^2	0.774	0.710	0.756	
$s^2_{residual}$	0.368	0.518	0.544	

Note: R^2 is the coefficient of determination and $s^2_{residual}$ is the variance of the residuals.

The Snowdon (1991) correction was used to back-transform predicted values. The exponentials of the predictions of the fixed model part should be multiplied by the Snowdon factors shown in Table 2 to correct the effect of logarithmic transformation of the predicted variable.

Models for mushroom species richness

The log-link function of the GLMM (eq. 3) to describe the dependence of the number of mushroom species on stand and site variables, as well as the year factors, was as follows:

$$[7] \quad \ln(p_{ij}) = b_0 + b_1 \times \ln(G_{ij}) + b_2 \times \sqrt{G_{ij}} + b_3 \times \ln(Ele_i) + b_4 \times \ln(Slo_i + 1) \times \cos(Asp_i)$$
$$+ a_1 \times Y_{1996} + a_2 \times Y_{1997} + a_3 \times Y_{1998} + a_4 \times Y_{1999} + a_5 \times Y_{2000} + a_6 \times Y_{2001} + a_7 \times Y_{2007} + u_i$$

where p_{ij} is the expected value of the number of mushroom species on 100 m² plot i in year j, G is stand BA (m²·ha⁻¹), Asp is aspect (rad), Slo is slope (%), Ele is elevation (m above sea level), Y_{1996}, Y_{1997}, ..., and Y_{2007} are fixed dummy variables of the corresponding years (the reference year is 1995, i.e., the parameter estimate of Y_{1995} is zero), and u_i is the random plot factor. The parameter estimates and the variance of the random plot factors are given in Table 2 together with some fitting statistics. The p values were less than 0.05 for all regression coefficients, except for some coefficients of the fixed year factors. The log-link function is nonlinear and causes bias in the predictions on the original scale. The exponential of the expected value should be multiplied by the Snowdon factor shown in Table 2 to correct the effect of logarithmic transformation.

The fixed year factors for years 1995, 1996, ..., 2001, 2007 (i.e., the parameter estimates of a values) were 0, −0.020, −0.261, −0.112, 0.564, 0.324, −0.260, and −0.303, respectively. The average annual number of mushroom species can be predicted using the sample mean of the fixed year factors (i.e., −0.009) as a year factor in eq. 7. The variance of the year factors was estimated from the sample variance of the fixed year factors (i.e., 0.074) by subtracting the additional variance caused by the estimation errors (Miina 1993).

The random plot factor was best explained by slope and dominant tree species in the stand. The ordinary least squares model to predict the plot factor was as follows:

$$[8] \quad b_i = b_0 + b_1 \times Slo_i^{1.5} + b_2 \times sylvestris_i + \varepsilon_i$$

where b_i is the plot factor predicted for plot i (see eq. 3), Slo is slope (%), "sylvestris" is a dummy variable equal to 1 for *P. sylvestris* stands and zero for *P. nigra* and *P. halepensis* dominated stands, and ε_i is the residual.
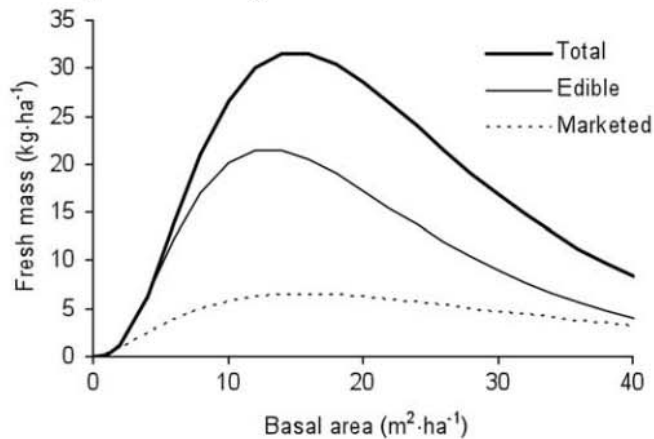
According to the model, the number of mushroom species is greatest when stand BA is near 20 m²·ha⁻¹ However, differently from the mushroom yield model, the decrease in the predicted number of species is less pronounced when stand BA is higher than 20 m²·ha⁻¹ (Fig. 6). Elevation and aspect affected the predicted number of species in the same way as in the mushroom yield model. When elevation increased from 500 to 1500 m, the number of species increased up to three times. A change in aspect from south to north increased the number of species up to two times. Slope, which is a predictor in the plot factor model, also had a very clear effect on the number of mushroom species. As the slope becomes steeper, the model predicts a smaller number of species. In addition, species richness is greater in *P. sylvestris* dominated than in *P. nigra* or *P. halepensis* dominated stands (Fig. 6).

The year factor correlated with autumn rain. The following model was fitted to describe the relationship (Table 3):

$$[9] \quad b_j = b_0 + b_1 \times AutumnRain_j + \varepsilon_j$$

where b_j is the year factor predicted for year j, "AutumnRain" is the total autumn rainfall (mm) during August, September, October, and November in year j, and ε_j is the residual.

Fig. 2. Mushroom production as a function of stand basal area and predicted plot factors (eqs. 4 and 5). Elevation was 1000 m, slope was 20%, and aspect was east–west. The dominant tree species was **Pinus nigra** or **Pinus halepensis**.

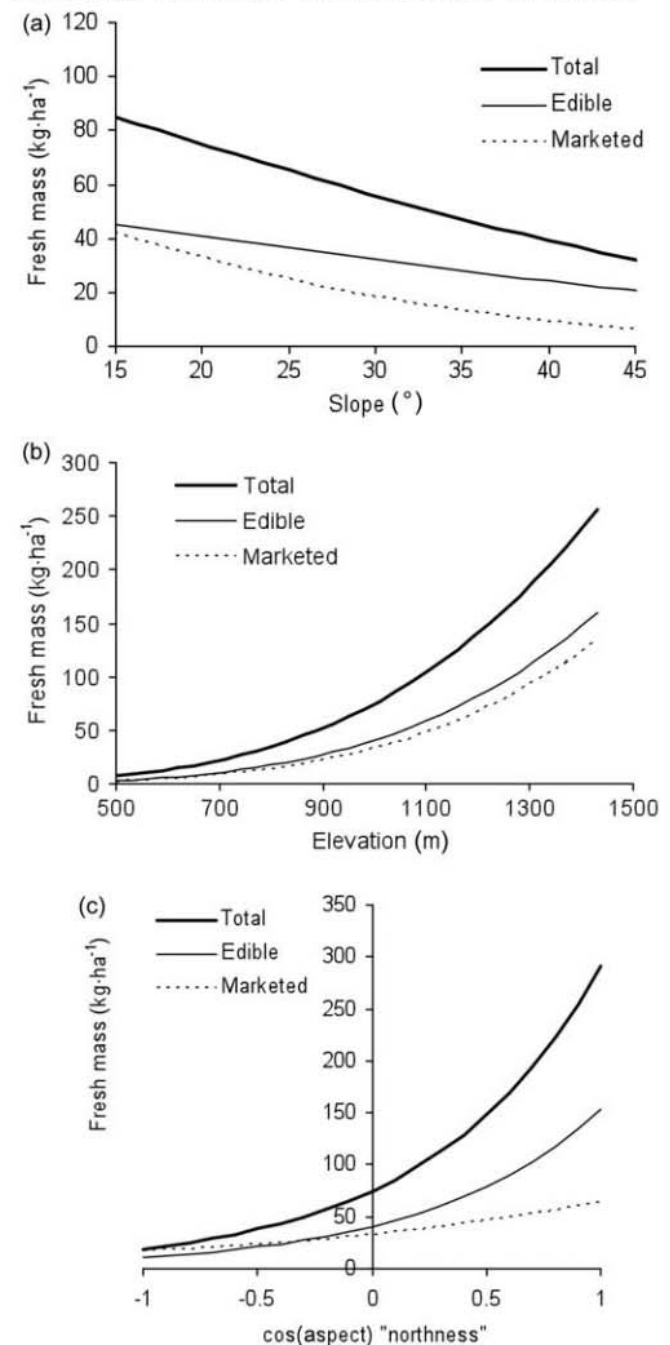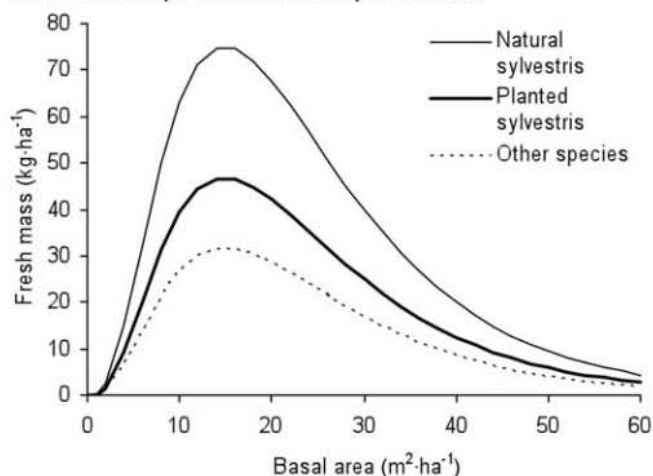**Fig. 3.** Mushroom production as a function of (a) slope, (b) elevation, and (c) aspect and predicted plot factors for natural **Pinus sylvestris** stands (eqs. 4 and 5). Stand basal area was 15 $m^2 \cdot ha^{-1}$, elevation was 1000 m, slope was 20%, and aspect was east–west.

Discussion

The decreasing economic returns from wood products in most forests of Mediterranean Europe threaten future investments in forest management. This threat may be decreased by including nonwood forest products in the analysis of the profitability of management alternatives. When considering the values of forest products, such as trees or mushrooms, we often think of them separately, without considering that when one product is harvested form the forest, most noticeably trees, the other resources are affected as well (Alexander et al. 2002). Integration of the relationships between various forest products is essential to optimize multiple-use forestry. Empirical models for predicting the production of nonwood forest products and for demonstrating the relationships between forest products and stand site variables are very useful tools for forestry optimization.

The modelling data used have some limitations. The number of plots for different tree species, sites, and stand ages was unbalanced, and the number of P. nigra and P. halepensis plots was small. Therefore, it is important to extend the network of mushroom plots in the future to cover all three tree species as well as different sites, stand ages, and stand densities more uniformly.

The developed models incorporate the stochastic between-plot and between-year structure to account for nested structures in the data (Fox et al. 2001), which otherwise would have resulted in biased standard error estimates of parameters. The models developed for the plot and year factors provide additional information about mushroom production and enhance the use of the models in prediction. Incorporation of the plot and year factors in the models improved the estimation efficiency, since each measurement brought information to the model, independent of other measurements (Fox et al. 2001).

The models revealed that stand BA was the strongest predictor of mushroom productivity. Interestingly, the highest mushroom productivity occurs at relatively low BA ranging from 15 to 20 $m^2 \cdot ha^{-1}$ (Fig. 4) in all three studied pine species. The BA associated with maximum mushroom productivity (Fig. 4) coincides with the peak of annual BA increment in these pine forests, which takes place at stand ages of around 20–40 years, suggesting that the resources needed for tree growth and for sporocarp production come from a common pool.

The majority of the sporocarps found in investigated forests are the fruitbodies of EMF that grow in symbiosis with the host trees. Kuikka et al. (2003) demonstrated the positive relationship between the photosynthetic capacity of the host tree and EMF fruitbody production by artificially defoliating

Fig. 4. Total mushroom production as a function of stand basal area, dominant tree species, and, for **Pinus sylvestris**, differentiated by natural or plantation-established stands (eqs. 4 and 5). Elevation was 1000 m, slope was 20%, and aspect was east.


Fig. 5. Total mushroom production as a function of total autumn rainfall in a north and south aspect of natural **Pinus sylvestris** stands (eqs. 4, 5, and 6). Stand basal area was 15 m²·ha⁻¹, elevation was 1000 m, and slope was 20%.
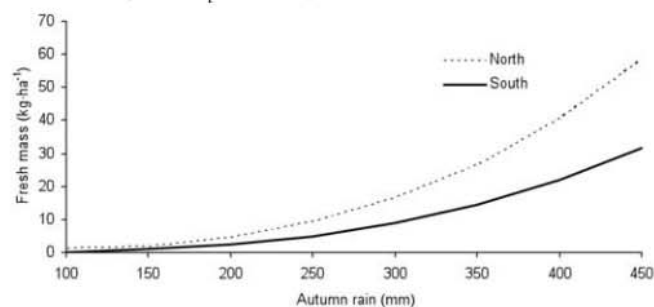
trees in a P. sylvestris forest for 2 years. Their results showed a threefold decline in ectomycorrhizal sporocarp production following defoliation as well as a reduction in sporocarp diversity in these treatments. Similar positive relationships between host photosynthetic rate and EMF sporocarp production (Bhupinderpal-Singh et al. 2003; Nara et al. 2003; Saravesi et al. 2008) help to explain our observation that when BA reaches the maximum annual increment, sporocarp production is also at its maximum.

Controlling stand BA through thinnings may be a useful tool to manage mycological resources. However, thinnings have multiple implications depending on the intensity, periodicity, and type of thinning. Luoma et al. (2004) examined the response of EMF sporocarps to four levels of BA removal with two patterns, either aggregated or dispersed. They reported that sporocarp production declined severely in heavy thinnings and even more when the thinning was aggregated. On the other hand, Pilz et al. (2006) found that the initial reduction of Canterellus formosa sporocarps in heavily thinned stands was negligible after 6 years. Shaw et al. (2003) applied a 50% thinning treatment to a 12-year-old P. sylvestris stand and found only minor effects on EMF

Fig. 6. Dependence of the number of mushroom species per year on stand basal area for **Pinus sylvestris** stands and other dominant tree species (**Pinus nigra** or **Pinus halepensis**) (eqs. 7 and 8). Elevation was 1000 m, slope was 20%, and aspect was east–west.
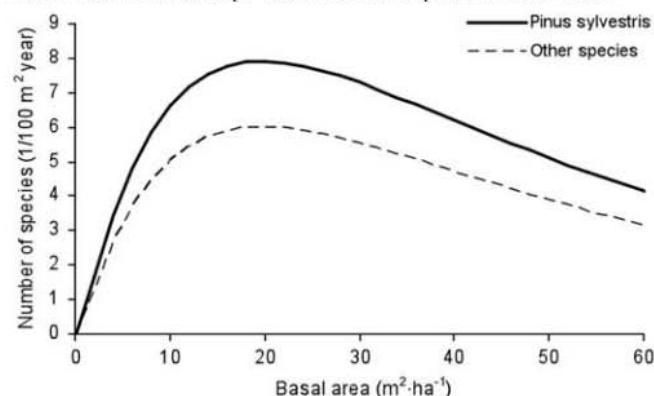
species composition. More research is needed to separate the effects of thinning from the effect of the BA in the stand.

Unlike stand BA, which can be managed, most of the other predictors for mushroom productivity detected in our study, namely slope, elevation, and aspect, cannot be modified and therefore would not help silviculturalists in the management of a certain stand. However, knowledge of these relationships is useful in landscape-level planning to identify stands whose primary income-generating products could be mushrooms.

The sharp increases in productivity that the models predict for higher elevations and for north-facing forests are likely to be related to water availability (Fig. 5). Water is the most limiting growth factor in the forests of the southern Central Pyrenees where light is abundant and temperatures are mild year-round. Higher productivity with higher elevations is a reflection of this very particular Mediterranean-influenced situation and cannot be generalized. We had no plots above 1528 m, so we cannot identify up to what elevation this relationship applies before production will be reduced due to colder temperatures, steep slopes, and lower site qualities.

The models predict higher mushroom productivity for naturally regenerated P. sylvestris stands when compared with plantations. However, more research is needed to verify this observation and to determine if the result is due to some unobserved variables.

Another result that requires more research is the clear difference between production in P. sylvestris stands and that in P. nigra and P. halepensis stands. The majority of the P. sylvestris stands are at higher elevations than those of P. nigra and P. halepensis. In the future, it would be important to better separate the site effects from the tree species effects. To do this, more balanced data are needed in which different species grow in similar sites.

Stand age is correlated with mushroom production but was not a significant predictor when stand BA was included in the model. Exclusion of stand age from the model may be regarded as an advantage, since most pine forests in the southeastern Pyrenees are managed as uneven-aged stands in which stand age is "undefined". However, stand age has

been shown to be an important predictor in British Columbia, Canada, where forest planners have used stand data and biogeoclimatic classification to map out habitat for multiple nonwood forest products. To predict ideal habitat for the highly valuable mushroom C. formosa, they have identified stand age, dominant tree species, and climatic zone to be the most reliable predictors of C. formosa production, with estimates in close agreement with field observations (Berch et al. 2006).

Maintaining biological diversity is one of the main challenges of the 21st century. Although land managers are interested in maintaining biodiversity, the methodology to do so is not always available. This is particularly important in temperate, Mediterranean-influenced forests like ours with very few tree species and hundreds of species of EMF that produce edible sporocarps. Our model of EMF species richness is an attempt to provide managers with a tool to maintain diversity. The model provides general guidelines but is still very limited because our data set only allowed us to use single-year species richness, which is in turn related to weather data. Nonetheless, as with the mushroom production model, we see that species richness is greatest at the peak of annual BA increment. The fact that species richness seems to be better correlated with stand structure than age is very important because it would allow us to manage mycodiversity by controlling stand structure. The model presented can be used to see the effects of different forest management alternatives in terms of fungi species richness, which can be an additional biodiversity indicator in operational management.

Species richness is related to elevation and aspect in the same way as mushroom productivity. This positive association between diversity and productivity in mushroom-forming fungi is of high relevance because it expands the theoretical work on the positive relationship between biodiversity and ecosystem productivity based on studies of vascular plants (Loreau et al. 2001, their fig. 4B) into the Kingdom of Fungi.

We must take with caution the projections of the model regarding the relationship between species richness and pine species because the three species of pine studied are not uniformly distributed over our studied landscape, and our data do not allow us to fully differentiate the effects of the pine species from the effects of site variables on mushroom productivity or species richness.

The models presented here, although needing further refinement, provide an initial tool for land managers to begin to incorporate mushroom production in the analyses carried out in forest planning. We expect that as more data become available and as models provide species-specific information for trees and mushrooms, mycological resources will become routinely incorporated into forest yield models, making it possible to take mushrooms into account when analysing the economic returns of investments in forestry.

Acknowledgements

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