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ARTICLE

RESEARCH ARTICLE

Wild mushroom productivity in timber plantations: a case study of *Pinus radiata* in Galicia, north-western Spain

Productividad de setas silvestres en plantaciones madereras: un caso de estudio en *Pinus radiata* en Galicia

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Abstract: *Aim of study*: (i) to evaluate wild mushroom productivity in a fast-growing *Pinus radiata* D.Don stand managed under four thinning treatments; (ii) to determine allometric relationships for seven mushroom species as a tool for future non-destructive inventory of fresh weight yield; and (iii) to compare the total productivity of two species of *Boletus* for three classes of sporocarp quality and the relationship with fruit development and size. *Area of study*: *Pinus radiata* thinning trial, Bóveda Communal Forest, Begonte, Galicia, north-western Spain. *Material and methods*: The productivity of seven marketable and two additional edible wild mushroom species was evaluated in a thinning trial in a *Pinus radiata* D.Don stand aged 32 years at the end of the observations. Sample plots of 20 × 20 m were evaluated over a period of 6 years (4 plots), 4 years (12 plots) and 2 years (12 plots). Four thinning treatments were applied in the plots: no thinning (control); light thinning from below; moderate thinning from below; and selective thinning. The mushroom inventories began 8 years after the last thinning operation. Average dimensions and allometric relationships of sporocarps were determined for seven mushroom species. The distribution of three quality classes of two *Boletus* species was also determined. Seasonal patterns of productivity of commercial species were established, with *Boletus pinophilus* Pilát & Dermek being the only species producing fruiting bodies in spring. *Main results*: The following marketable species were identified, in decreasing order of productivity: *B. pinophilus*, *Hydnum repandum* L., *Lactarius quieticolor* Romagn., *Imleria badia* (Fr.) Vizzini, *Boletus edulis* Bull., *Suillus luteus* (L.) Roussel and *Tricholoma portentosum* (Fr.) Quél. Two edible non-marketable species *Clitopilus prunulus* (Scop.) P. Kumm. and *Laccaria amethystina* Cooke were also identified. The total yield of edible species was 58.5 kg ha^{-1} year^{-1} and the thinning intensity did not have a significant effect on the total edible or marketable mushroom productivity, which was more affected by the distance of the plot relative to the edge with firebreaks. The average size of sporocarps, in terms of both weight and diameter, decreased in the following order: *B. pinophilus* > *B. edulis* > *S. luteus* ≈ *I. badia* > *Lactarius quieticolor* > *T. portentosum* > *H. repandum*. The quality of boletes was closely related to the cap diameter, with the probability of occurrence of fruiting bodies with white hymenium and firm flesh decreasing in sporocarps larger than 7-8 cm. Quality classes 1 and 2 tended to be maintained for larger sizes of *B. edulis* than of *B. pinophilus*. Overall, 51% of the fresh weight of *B. pinophilus* harvested was classified in classes 1 or 2, whereas the corresponding figure was 69% for *B. edulis*. *Research highlights*: Mushroom productivity in the radiata pine stand under study was similar to the average values obtained for native pine species in Spain and may be relevant to the management of these fast-growing plantations.

Keywords: forest management; mushroom productivity; *Pinus radiata*; sporocarp allometry; sporocarp quality.

Resumen: *Objetivos del estudio*: (i) evaluar la productividad de setas silvestres en un rodal de crecimiento rápido de *Pinus radiata* D.Don sujeto a cuatro tratamientos de clara (ii) proporcionar relaciones alométricas para siete especies de hongos como una herramienta para futuros inventarios no destructivos de la producción en peso fresco y (iii) determinar para dos especies de *Boletus* la distribución de la productividad total entre tres clases de calidad de los esporocarpos y su relación con el desarrollo y dimensión de los mismos. *Área del estudio*: sitio de ensayo de clara de *Pinus radiata*, Monte Vecinal en Mano Común de Bóveda, Begonte, Galicia, noroeste de España. *Material y métodos*: La productividad de siete especies comercializables y dos especies adicionales comestibles fue evaluada en un sitio de ensayo de claras de pino radiata que contaba con 32 años en el momento final de las observaciones. Para ello, se evaluaron 4 parcelas de 20 × 20 m por un periodo de 6 años, 12 parcelas durante 4 años y 12 parcelas durante 2 años. Se aplicaron cuatro tratamientos de clara: un control sin clara, una clara baja débil, una clara baja de peso moderado y una clara selectiva. Los inventarios micológicos comenzaron 8 años después de la última intervención de clara. Se determinaron las dimensiones medias de los carpóforos y relaciones alométricas para los esporocarpos de las siete especies comerciales, así como la distribución de tres clases de calidad para ambas especies de boletos. Se determinaron los patrones estacionales de productividad comercial, siendo *Boletus pinophilus* Pilát & Dermek la única especie que fructificó en primavera. *Resultados principales*: Las especies comerciales en orden de productividad fueron: *B. pinophilus*, *Hydnum repandum* L., *Lactarius quieticolor* Romagn., *Imleria badia* (Fr.) Vizzini, *Boletus edulis* Bull., *Suillus luteus* (L.) Roussel y *Tricholoma portentosum* (Fr.) Quél, con *Clitopilus prunulus* (Scop.) P. Kumm. y *Laccaria amethystina* Cooke como especies comestibles no comercializables. La productividad total de especies comestibles fue de 58.5 kg ha^{-1} $año^{-1}$ y no se obtuvo un efecto significativo del tipo de clara en la productividad, la cual estaba más afectada por la posición de cada parcela con respecto a los cortafuegos. El tamaño promedio de los esporocarpos mostró este orden, tanto para el peso fresco como para el diámetro del pileo: *B. pinophilus* > *B. edulis* > *S. luteus* ≈ *I. badia* > *Lactarius quieticolor* > *T. portentosum* > *H. repandum*. La calidad de las especies de boletos está muy relacionada con el diámetro del píleo, con baja probabilidad de encontrar esporocarpos de himenóforo blanco y carne firme para tamaños superiores a 7-8 cm. *B. edulis* mostró una tendencia a mantener calidades 1 y 2 para tamaños superiores a *B. pinophilus*. En general, el 51% del peso fresco recogido de *B. pinophilus* correspondía a calidades 1 o 2, mientras que ese valor fue de 69% para *B. edulis*. *Aspectos destacados de la investigación*: El nivel de productividad fúngica en el rodal de pino radiata estudiado fue similar a los promedios obtenidos para especies de pino nativas en España y pueden ser relevantes para la gestión de estas plantaciones de crecimiento rápido.

Palabras clave: alometría de esporocarpos; calidad de esporocarpos; gestión forestal; *Pinus radiata*; productividad fúngica.

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Supplementary information ↓

1. INTRODUCTION

Fungi provide a range of provisioning, regulating, supporting and cultural services in forest ecosystems, becoming fundamental to ecosystem maintenance (Pringle et al., 2011, Heilmann-Clausen et al., 2015; Peura et al., 2016). Among fungi, mycorrhizal species play an important role in forest nutrition and water uptake (Luoma et al., 2004), enhancing the growth and survival of symbiotic plants (Anthony et al., 2022), modelling soil properties and the storage of soil carbon (Clemmensen et al., 2013), and plant resistance to soil pathogens (Duchesne et al., 1989).

Plantation forests are primarily established for wood and fibre production. However, in recent years there has been growing interest in their multifunctional use, with wild mushroom production as one of the most important activities (Torres et al., 2021). Wild forest mushrooms are gaining attention among consumers in north-western Spain and some communal forests have implemented initiatives that limit mushroom harvesting (open or closed reserves, (Copena et al., 2022), thereby increasing opportunities to obtain economic and other benefits such as recreation or picking for personal consumption.

Radiata pine (*Pinus radiata* D.Don) is a major exotic timber species in northern Spain (Diéguez-Aranda et al., 2005), with plantations extending from Galicia to the Basque Country. Despite being native to North America, *P. radiata* has shown a good capacity to establish interactions with European fungal species (Sarrionandia et al., 2015). Mycorrhization of radiata pine plants can occur spontaneously in nurseries, and artificial mycorrhization is also conducted in Spanish forest nurseries, but using species that are not widely consumed. The productivity of these fungal habitats is therefore currently derived from wild species of mushrooms.

Understanding the factors affecting mushroom yield would enable the application of silvicultural methods aimed at the joint production of timber and mushrooms (Martínez-Peña et al., 2011; Tahvanainen et al., 2016; Tomao et al., 2017). Forest plantations can also be managed to increase the productivity of ectomycorrhizal fungi, with the possibility of cultivation throughout controlled mycorrhization (Savoie & Largetau, 2011; Guerin-Laguette et al., 2014). The importance of mushroom productivity in fast-growing plantations has seldom been studied in Europe, particularly regarding exotic species.

Based on these considerations, the aims of this paper are: (i) to evaluate the marketable and most relevant edible wild mushroom productivity in a fast growing radiata pine stand managed under four thinning types (ii) provide allometric relationships for seven mushroom species as a tool for future non-destructive inventory of fresh weight yield and (iii) determine for two species of *Boletus* the distribution of total productivity among three classes of sporocarp quality and their relationship with fruit development and size.

2. MATERIAL AND METHODS

2.1. Site conditions and the thinning trial

The study area is located in Begonte, Galicia, NW Spain (43°8’60”N 7°45’5”W, with a mean elevation of 455 m a.s.l.). The lithology of the area includes phyllites alternating with schists. The soils, classified as Regosols are moderately deep (A-Bw-C profile), with a high organic matter content in the A horizon (11.0%, sd=1.3%, n=24 samples), a low degree of stoniness and a predominantly clay-loam or loam texture (average 25% sand, 46% silt and 29% clay). The average soil pH value was 4.9 (sd = 0.1), which is rather high for the generally acid soils in the region. The average C/N ratio was 17 (sd = 1.6%). The cation exchange capacity was very low (average 5 cmol(+) kg^{-1}, sd = 1.25) and with a very high degree of Al saturation (79%).

The mean annual rainfall during the study period was 1435 mm and peaked in December and January with more than 200 mm of rainfall in each month. Mean temperature was 12.0 °C (max: 17.7 °C in August; min: 6.5 °C in January) (Sambreixo meteorological station, www.meteogalicia.gal).

The thinning trial is in a *Pinus radiata* plantation established in the spring of 1992 with a 3×3 m spacing using two-year old bare-root seedlings with spontaneous nursery mycorrhization. Two provenances of the species were planted: a genetically improved seed lot from New Zealand, and an unimproved local commercial lot of seeds (Galician introduced provenance). A thinning trial was established when the plantation was 12 years old and included four treatments with three repetitions for each provenance and plots of 30×30 m, following a completely randomised design. Two thinning interventions were applied at ages 11 and 18 years, according to the parameters shown in Table 1, corresponding to the following thinning treatments (Gonçalves, 2021):

- No thinning (control).
- Thinning from below of light intensity (less than 20% of basal area removed in each intervention).
- Thinning from below of moderate intensity (25-30% of basal area removed).
- Selective thinning promoting future trees by thinning competitors from above at moderate intensity (25-30% of basal area removed).

Table 1. Thinning treatments applied in the *Pinus radiata* D.Don stand trial

Treatment	Thinning at 11 years				Thinning at 18 years			
	RN (%)	SG	RV (%)	V_{eu} (dm^3)	RN (%)	SG	RV (%)	V_{eu} (dm^3)
Control	0.8	-	0.6	30	0	-	0	0
Light thinning from below	26.8	0.36	9.7	31	40.4	0.44	17.6	168
Moderate thinning from below	43.9	0.46	20.0	40	51.1	0.55	28.3	224
Selective thinning	28.7	0.78	22.3	70	35.5	0.69	24.6	272

RN: ratio of trees removed. SG ratio is the percent of trees removed divided by the percent of basal area removed. RV is the ratio of volume removed. V_{eu} is the unit volume of trees removed.

A buffer zone of 3 lines of trees was included between plots and at the stand edge, so that the distance from the edge of the timber plots to the 12 m wide forest fire breaks surrounding each compartment was at least 10 m.

2.2. Stand attributes and mushroom productivity plots

The inventory of the 24 forest plots was performed in January 2024, when the stand was 32 years old, i.e. 14 years after the second thinning. The diameter at breast height (d, cm) of each standing tree was cross measured to the nearest 0.1 cm. Total tree height (h, m) was measured to the nearest 0.1 m using a Vertex III hypsometer. The status of each tree (e.g. living or dead; damaged or undamaged) was also recorded.

Dominant height, site index (calculated at a reference age of 20 years), tree density (N), standing dead trees (DT), basal area (G), Hart-Becking stand density index (HBI, average distance among trees as a percentage of dominant height) and the stand management indicator (SMI, ratio between basal area of the sampled year and tree density) were computed for all the plots (Diéguez-Aranda et al., 2005; Herrero et al., 2019). The New Zealand provenance show a clear advantage both in terms of dominant height (34.9, sd = 1.14 versus 32.1, sd = 1.36) and site index: (26.5 m, sd = 0.98 versus 24.0, sd = 1.17). The differences in terms of N, G, DT, HBI and SMI were mainly attributable to the thinning treatments (Table 2). Overall, the values of HBI and G indicate that the stand is very well stocked and there has been a long period without thinning. The average mean annual increment of timber is 20.4 m^3 ha^{-1} $year^{-1}$, which indicates a high level of productivity for the region.

Table 2. Stand attributes depending on the thinning treatment applied (n = 6 for each treatment)

Treatment	N (trees ha^{-1})	G (m^2 ha^{-1})	DT (%)	HBI (%)	SMI (m^2 $tree^{-1}$)
Control	769a (113)	52.7a (6.4)	31.0 a (1.6)	11.0c (0.9)	0.0693c (0.092)
Light thinning from below	524b (30)	47.6ab (5.6)	24.4 a (5.0)	12.8b (0.4)	0.0908b (0.0083)
Moderate thinning from below	417b (39)	45.8ab (5.2)	9.5 b (5.5)	14.8a (1.1)	0.1107a (0.0155)
Selective thinning	426b (61)	41.1b (4.2)	17.0 c (4.3)	14.6a (0.3)	0.0982b (0.0165)

N: tree density, G: basal area, DT: percentage of mortality in standing trees, HBI: Hart-Becking index and SMI: stand management indicator. Standard deviation in brackets. Letters denote significant differences among means in the same columns according to the Tukey test.

In 2019, four 20×20 m sampling plots (one per each thinning type) were established in the New Zealand provenance. The number of plots was increased to 12 in 2021 to encompass the three repetitions of each thinning for this provenance. In 2023, an additional 12 plots were established to cover the Galician provenance, to yield a total of 24 sampling plots (see Figure 1). Tending the plots involved yearly cutting of the understorey vegetation, which was dominated by brambles.

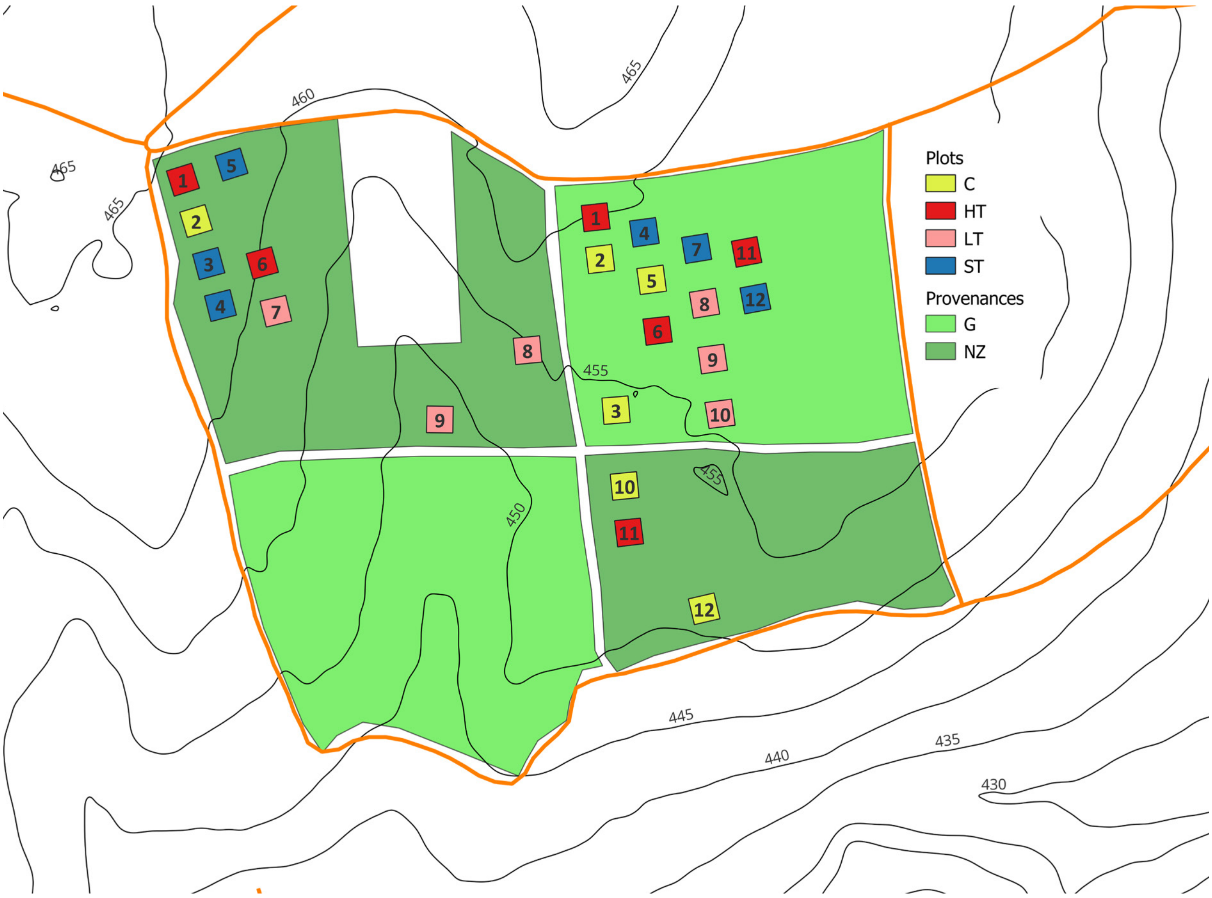

Figure 1. Experimental design of the 20×20 m mushroom sampling plots in stands of the two different radiata pine provenances in Bóveda, Begonte, Lugo, Spain, showing the plot identification numbers and the thinning treatment applied. The positions of the plots relative to the stand edge can be observed.

The distance between plots and the compartment edge may be an additional factor to be considered (Figure 1). This distance (D) was calculated as the average distance between each of the four corners of the sample plots and the edge. The value of D varied widely, ranging from 16.5 to 90 m (0.5 to 2.5 times the dominant height), with average of 43 m and a coefficient of variation of 53%.

Plot sampling frequency was weekly from September to February (autumn and winter) and every two weeks from March to May (spring productivity), considering the productive season from September to the end of the following year's spring. Only the sporocarps of the marketable species (according to the Spanish Decree 30/2009) were collected, including *Boletus pinophilus* Pilát & Dermek, *Boletus edulis* Bull., *Lactarius quieticolor* Romagn., *Hydnum repandum* L., *Imleria badia* (Fr.) Vizzini, *Suillus luteus* (L.) Roussel and *Tricholoma portentosum* (Fr.) Quél. Moreover, two edible species of interest were included: *Clitopilus prunulus* (Scop.) P. Kumm. and *Laccaria amethystina* Cooke. Sampling frequency captured the average duration of the fruiting bodies, which can be very short-lived (*Lactarius, Boletus*) or quite long-lived (*Hydnum*) (Moore et al., 2008). All fruiting bodies larger than 2 cm (*Hydnum, Lactarius* and *Tricholoma*), 3 cm (*Imleria*) and 4 cm (*Boletus*) were counted and harvested. The sporocarps were weighed fresh and the cap diameter was measured. To cover the whole range of cap diameters, additional sporocarps with large diameters were collected outside the plots.

The productivity of the seven species mentioned was determined for each season by summing the fresh weight of the sporocarps collected in each plot and scaling-up the value to a hectare using a factor of 25. Additional response variables included the productivity of total marketable species (7) and the productivity of all edible species (9), evaluated per plot and season.

For both boletes, the sporocarps were also categorised according to their marketability, in three quality classes:

- Quality 1 (Q1). Sporocarps with white hymenium and firm flesh in cap and stipe.
- Quality 2 (Q2). Sporocarps with cream-yellow hymenium and less firm flesh in the stipe.
- Quality 3 (Q3). Sporocarps with green hymenium, firm flesh and insect infestation restricted to the stipe base.

2.3. Statistical analysis

The data were processed to determine the mean values and dispersion measures of response variables. In the case of the fungal productivity variables, analysis of covariance (ANCOVA) was performed, considering the average distance to the plantation edge as a covariable. One-way and two-way ANCOVA were used to determine any significant effects of the treatment, the provenance or the plot location on the productivity of single species, the total commercial productivity and the total edible productivity. Pairwise comparisons were conducted using Tukey's test to examine all possible differences between treatments or plot locations, considering the least squared adjusted means.

Pearson's correlation coefficients were calculated to evaluate the relationships between productivity response variables and stand attributes. Test results were considered significant at $p < 0.05$. To evaluate interannual variability, the coefficient of variation, ratio between the mean and the standard deviation of yearly values, was employed.

The cap weight was estimated considering the cap diameter as the predictive variable and using an allometric equation (Eq. 1). The iterative Gauss-Newton method was used to estimate both parameters, with starting values of the parameters proposed from the log-linear fitting. Parameter estimates were considered significant at $p < 0.05$.

$$\hat{y} = a_0\, d^{a1} \qquad (1)$$

As some heteroscedasticity was detected in the residual plots, we used a potential function of the cap diameter as the weight of each observation. The value of the exponent k was obtained using the approach proposed by Harvey (1976) of using the residuals of the model fitted without weights as a dependent variable in the potential model of error variance (Álvarez-González et al., 2007).

To evaluate the goodness-of-fit of the models, we used the mean residual (BIAS) as a measure of accuracy and the root of mean square error (RMSE) to define the precision. Predicted and observed values were visually plotted to assess the accuracy and precision of the models. All analyses were performed using the R statistical package (R Core Team, 2020).

3. RESULTS

3.1. Mushroom productivity: spatial and interannual variability

The average productivity of commercial mushroom species determined using the plot-average values (n = 24) was 55.3 kg ha^{-1} year^{-1} (σ = 27.7 kg ha^{-1} year^{-1}). This value increased slightly, to 58.5 kg ha^{-1} year^{-1}, when the two additional edible species (*C. prunulus* and *Laccaria amethystina*) were considered. The contribution of each species to the productivity is shown in Table 3. *B. pinophilus* contributed most to the productivity. Overall, the average productivity of both boletes reached 23 kg ha^{-1} year^{-1}. The high level of interplot variability reflected a high spatial variation in mushroom yield; the coefficient of variation for each species was always higher than 100%. The minimum productivity is 0 for all the species, indicating null production for one of the species considered in at least one of the 24 plots. *H. repandum* was the species more widely distributed among the plots.

Table 3. Mushroom productivity (kg ha^{-1} $year^{-1}$) by species (average of n=24 plots). Minimum and maximum values for n = 24 plots are provided

Species	Average	σ	Minimum	Maximum	Plots with null production
Boletus pinophilus	18.4	18.8	0	64.3	3
Hydnum repandum	13.4	15.2	0	47.4	1
Lactarius quieticolor	9.5	12.6	0	48.4	4
Imleria badia	5.8	6.0	0	20.5	3
Boletus edulis	4.7	5.5	0	23.6	3
Suillus luteus	3.1	4.9	0	16.5	9
Tricholoma portentosum	0.35	0.71	0	2.79	15
Clitopilus prunulus	3.0	5.4	0	25.3	2
Laccaria amethystina	0.25	0.40	0	1.43	11

σ denotes the standard deviation.

The ANCOVA applied to the two seasons where data was available for the 24 plots indicated significant negative effects of the distance to the forest edge on the commercial mushroom productivity ($p = 0.0004$), on the total edible biomass productivity ($p = 0.0005$) and on *H. repandum* productivity ($p = 0.0003$). The pine provenance was only a significant factor for the *H. repandum* ($p < 0.0001$) and *S. luteus* productivity ($p = 0.0469$), in both cases with higher values for the Galician provenance (20.1 kg ha^{-1} $year^{-1}$ versus 11.5 kg ha^{-1} $year^{-1}$ for *H. repandum*, 5.1 kg ha^{-1} $year^{-1}$ versus 0.6 kg ha^{-1} $year^{-1}$ for *S. luteus*).

The thinning treatment did not significantly explain commercial productivity, although the least square means classification showed that mushroom productivity was lowest in the unthinned control plots and significantly lower than the heavily thinned plots ($p = 0.0405$). In the case of *B. pinophilus*, the treatment had a significant effect ($p = 0.0849$), showing significant differences of lsmeans between a first group of two treatments (heavy and selection thinning) and a second group (light thinning and the control).

The *Lactarius quieticolor* productivity was not affected by the distance to the forest edge and the treatment effect was clearly significant in this species ($p=0.0098$), with light thinning (25.7 kg ha^{-1} $year^{-1}$) having a clear advantage over the selective and heavy thinning (7.0 and 6.1 kg ha^{-1} $year^{-1}$) and the unthinned control yielding a very low value (3.0 kg ha^{-1} $year^{-1}$).

The only relationship between stand variables and productivity was the one involving the stand management indicator. SMI was significantly related (n = 80 observations) to the productivity of total edible species ($\rho = 0.307$, $p = 0.0056$), the productivity of commercial species ($\rho = 0.267$, $p = 0.0166$) and *B. pinophilus* productivity ($\rho = 0.239$, $p = 0.0327$).

Regarding the relationships between the level of productivity of different species, we found that *B. pinophilus* productivity was significantly negatively related to *Lactarius quieticolor* productivity ($\rho = -0.279$, $p = 0.0123$) and positively related to *C. prunulus* ($\rho = 0.260$, $p = 0.0196$) and *S. luteus* ($\rho = 0.258$, $p = 0.021$) productivity, being those relationship probably related to the plot conditions.

The interannual variability was studied in 4 plots in which productivity was available for a series of 6 seasons. The coefficient of variation for the total commercial yield was 52.7% (range 42.1 to 69.7). The year in which productivity was highest varied in the four plots (data not shown). The results for the average of 4-plot productivity for each commercial species are shown in Table 4. The *B. pinophilus* yield was the least affected by interannual changes of productivity. The variability was much higher for the less productive species. The seasons when productivity was highest did not coincide for the different species, and high levels of productivity were obtained in almost all seasons for a particular species.

Table 4. Productivity of the commercial mushroom species for six consecutive seasons (from 2019 to 2025). Average for n = 4 plots

Species	Season						CV (%)
	19/20	20/21	21/22	22/23	23/24	24/25	
Boletus pinophilus	19.0	18.6	24.1	44.0	40.9	20.4	41.4
Hydnum repandum	2.2	6.7	5.3	8.0	21.6	18.6	75.1
Lactarius quieticolor	7.8	5.4	4.2	4.9	2.1	1.7	51.8
Suillus luteus	13.9	32.8	5.0	9.0	11.1	9.5	72.8
Boletus edulis	4.0	1.8	0.9	1.8	2.7	0.0	74.5
Imleria badia	0.0	1.7	0.6	1.3	3.3	4.8	91.9
Tricholoma portentosum	0.9	3.2	0.3	2.5	1.0	0.0	96.0

CV denotes interannual coefficient of variation.

3.2. Mushroom productivity: seasonal patterns and sporocarp dimension

The seven commercial species showed a marked fructification pattern along the seasons (Figure 2). *I. badia*, *Lactarius quieticolor* and *B. pinophilus* can be considered early species, with fruiting bodies already appearing in the second half of September and peaking in production in the first half of October. Nonetheless, fructification of the pine bolete is more extended, with fruiting bodies emerging until the first half of January. After a couple of months without fructification, the spring productivity, particularly during April and May, accounted for roughly 10% of the seasonal productivity for this species.

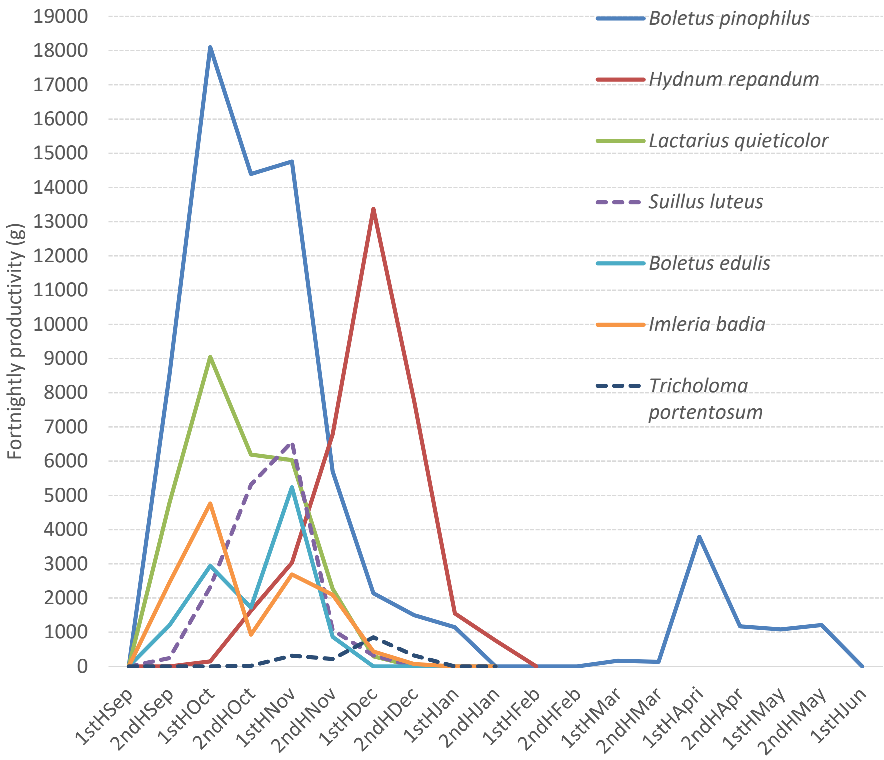

Figure 2. Fortnightly pattern of productivity along the productive season for the total amount of fruiting bodies (fresh weight) of the seven commercial species harvested in all the plots. 1stH refers to the first half of the month, 2ndH to the second half.

A similar pattern of fructification was observed throughout the season for *S. luteus* and *B. edulis*, with a peak occurring in the first half of November and a decline in fruiting coincident to the one of *I. badia* and *Lactarius quieticolor*. In *H. repandum* and *T. portentosum*, known as late-fruiting species, fruiting bodies emerged in the first half of October, with the peak productivity occurring in the first half of December. Collection of *H. repandum* was even possible in the second half of January, indicating the durability of its fruiting bodies (see Figure 2).

Analysis of the size of the sporocarps of the commercial species showed that the thinning treatment did not significantly affect the weight or the diameter of the commercial species. Average values and variability measures for diameter and weight of each species are shown in Table 5. Both boletes had the largest sporocarps, whereas *H. repandum* has the smallest (Table 5). Both the weight and diameter decreased in the order *B. pinophilus* > *B. edulis* > *S. luteus* ≈ *I. badia* > *Lactarius quieticolor* > *T. portentosum* > *H. repandum*. The same order was observed for the maximum weight and diameter measured. Ranges are very broad for weight and diameter in all the species. As can be expected, the cap diameter and the fresh weight were closely related, which enabled the development of regression equations that could be used for non-destructive inventory of sporocarps. Intraspecific variability was nevertheless high for the different species, as shown in Figures 3-9, in which the quality classes of boletes for each paired cap diameter - fresh weight observation are also shown.

Table 5. Average size of fruiting bodies of the commercial species collected in the plots

Species	Sporocarp weight (g)			Sporocarp diameter (cm)		
	Average	σ	Range	Average	σ	Range
Boletus pinophilus	184.8	142.8	9-1329	8.85	3.34	4-25
Hydnum repandum	12.3	8.1	1-67	4.25	1.73	2-12
Lactarius quieticolor	24.1	16.8	1-121	6.38	3.85	2-13
Imleria badia	46.8	32.8	7-252	6.79	2.22	3-13
Boletus edulis	134.1	95.4	11-651	8.28	3.13	4-17
Suillus luteus	47.6	37.6	4-177	6.63	2.20	2-12
Tricholoma portentosum	21.6	12.5	4-59	5.5	1.4	2-9

σ denotes the standard deviation.

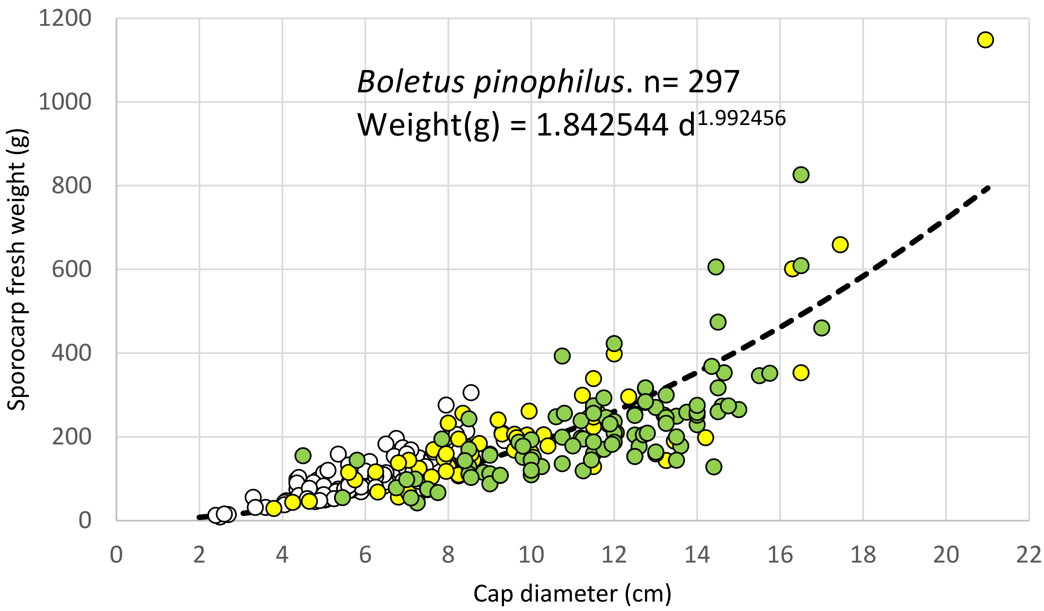

Figure 3. Plots of sporocarp weight versus cap diameter showing the fitted model for *Boletus pinophilus*. Quality 1 is represented by white circles, quality 2 by yellow circles and quality 3 by green circles. Note not all the sporocarps were evaluated for quality.

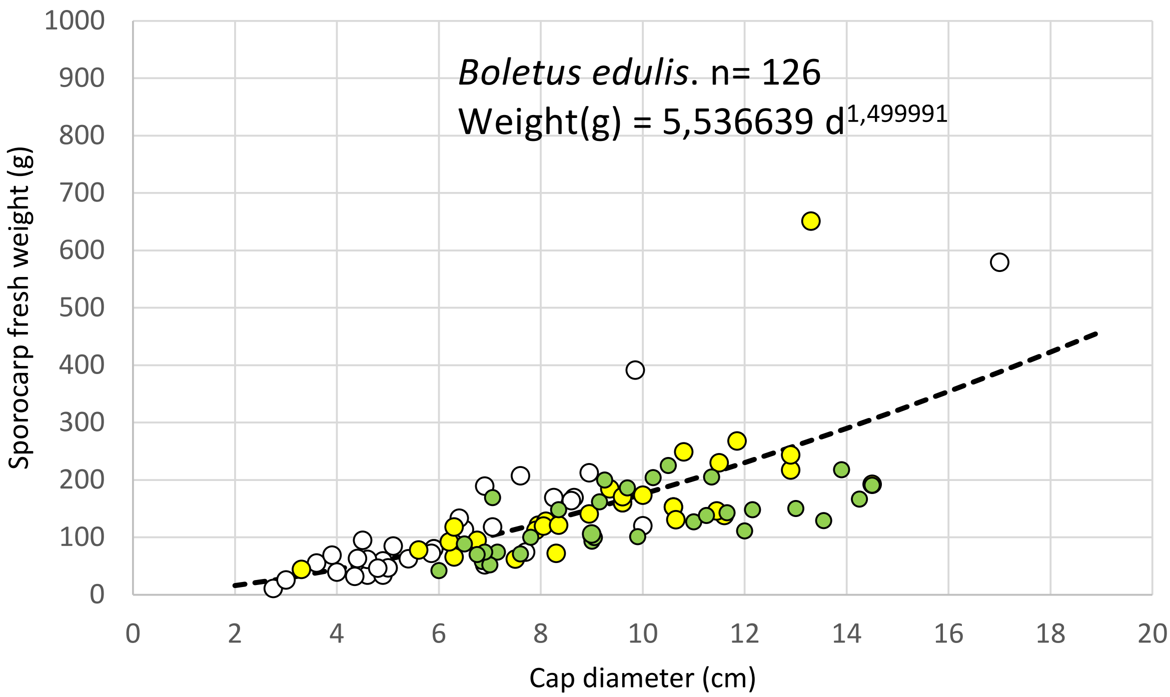

Figure 4. Plots of sporocarp weight versus cap diameter showing the fitted model for *Boletus edulis*. Quality 1 is represented by white circles, quality 2 by yellow circles and quality 3 by green circles. Note not all the sporocarps were evaluated for quality.

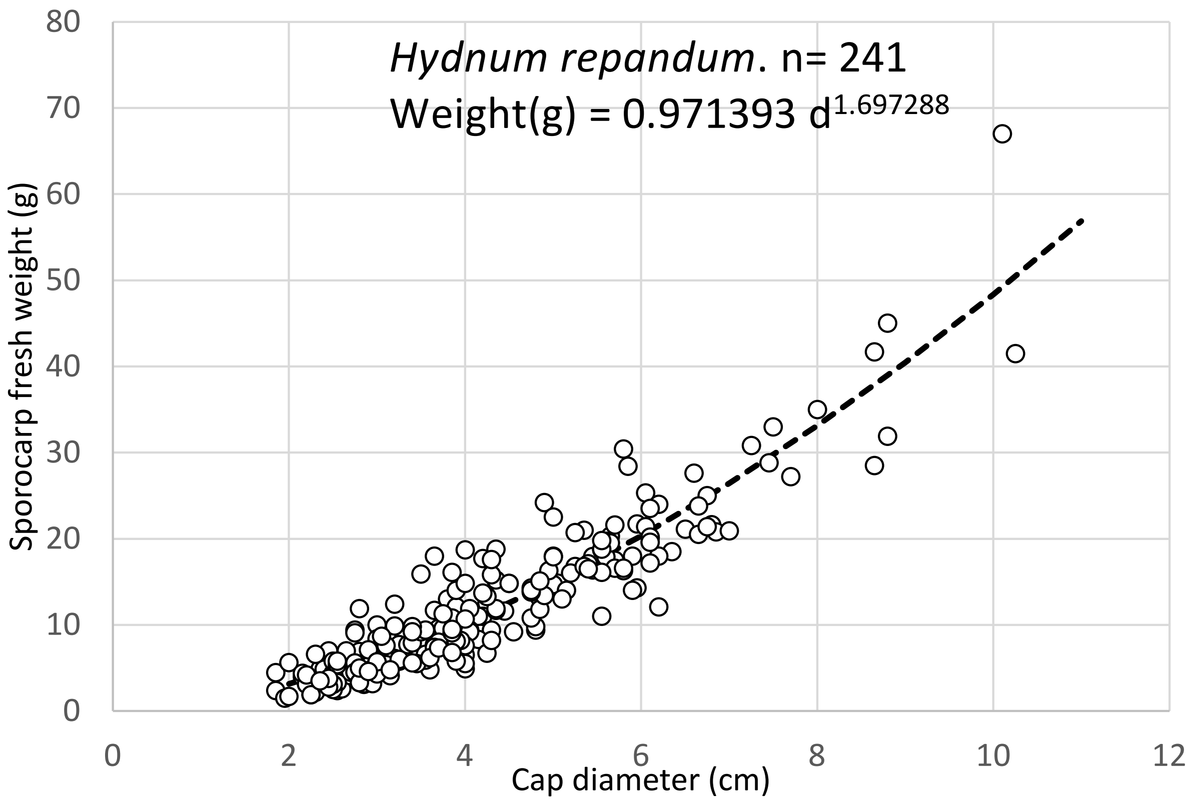

Figure 5. Plots of sporocarp weight versus cap diameter showing the fitted model for *Hydnum repandum*.

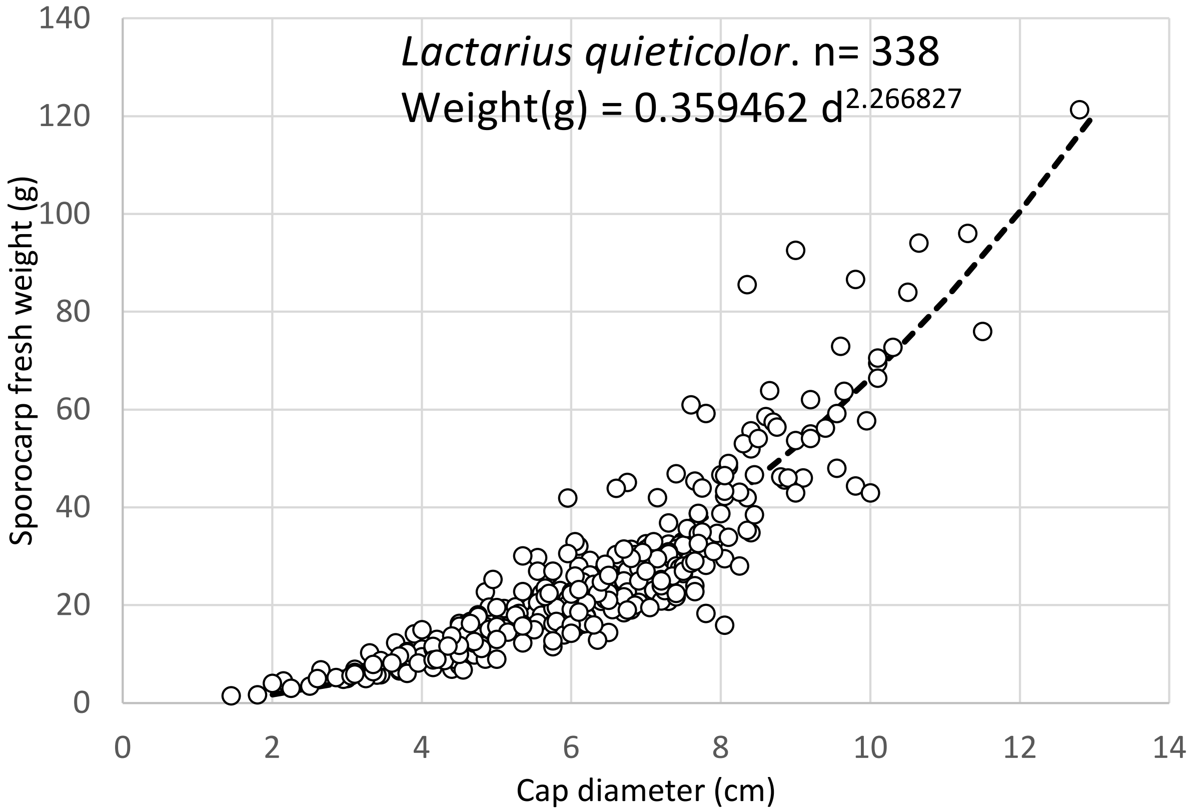

Figure 6. Plots of sporocarp weight versus cap diameter showing the fitted model for *Lactarius quieticolor*.

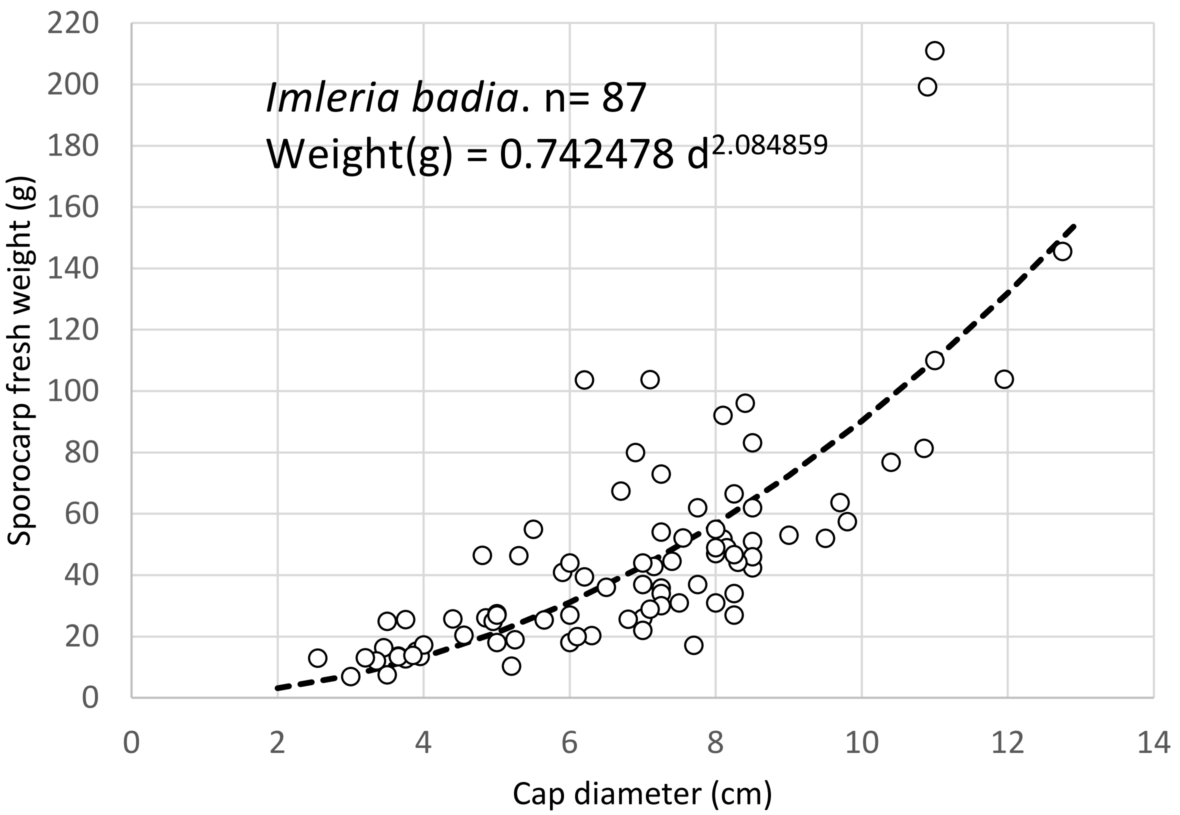

Figure 7. Plots of sporocarp weight versus cap diameter showing the fitted model for *Imleria badia*.

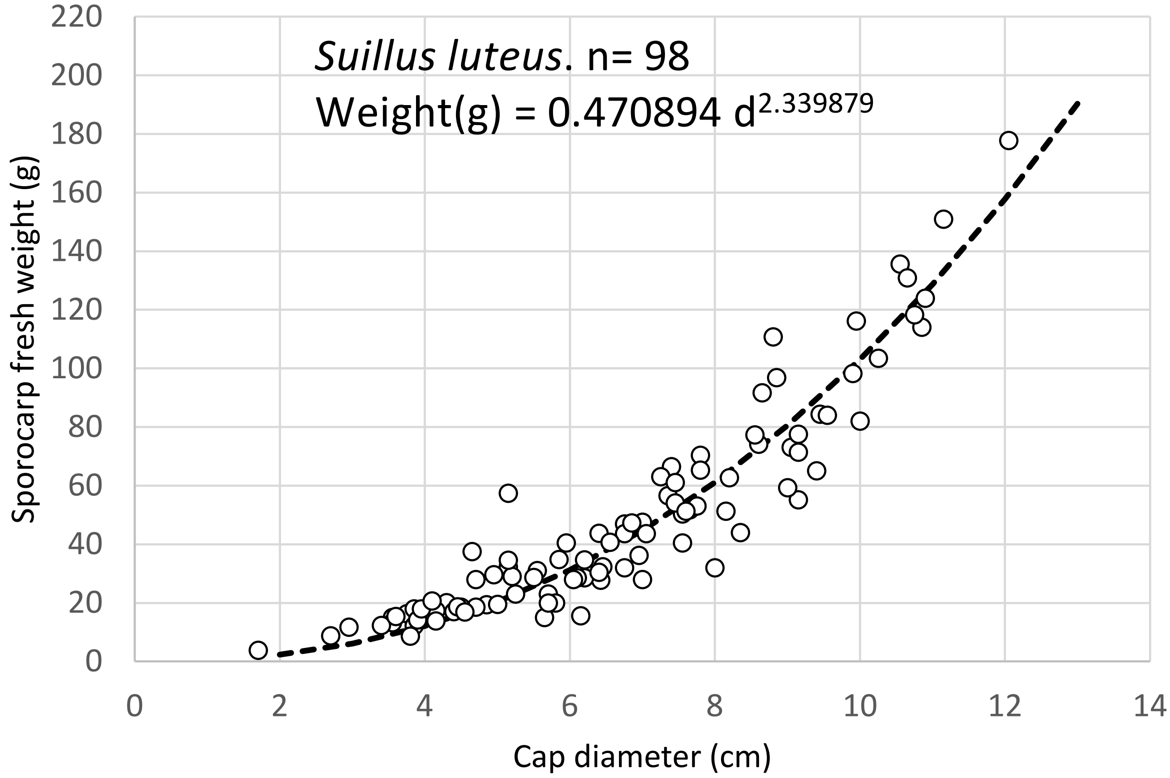

Figure 8. Plots of sporocarp weight versus cap diameter showing the fitted model for *Suillus luteus*.

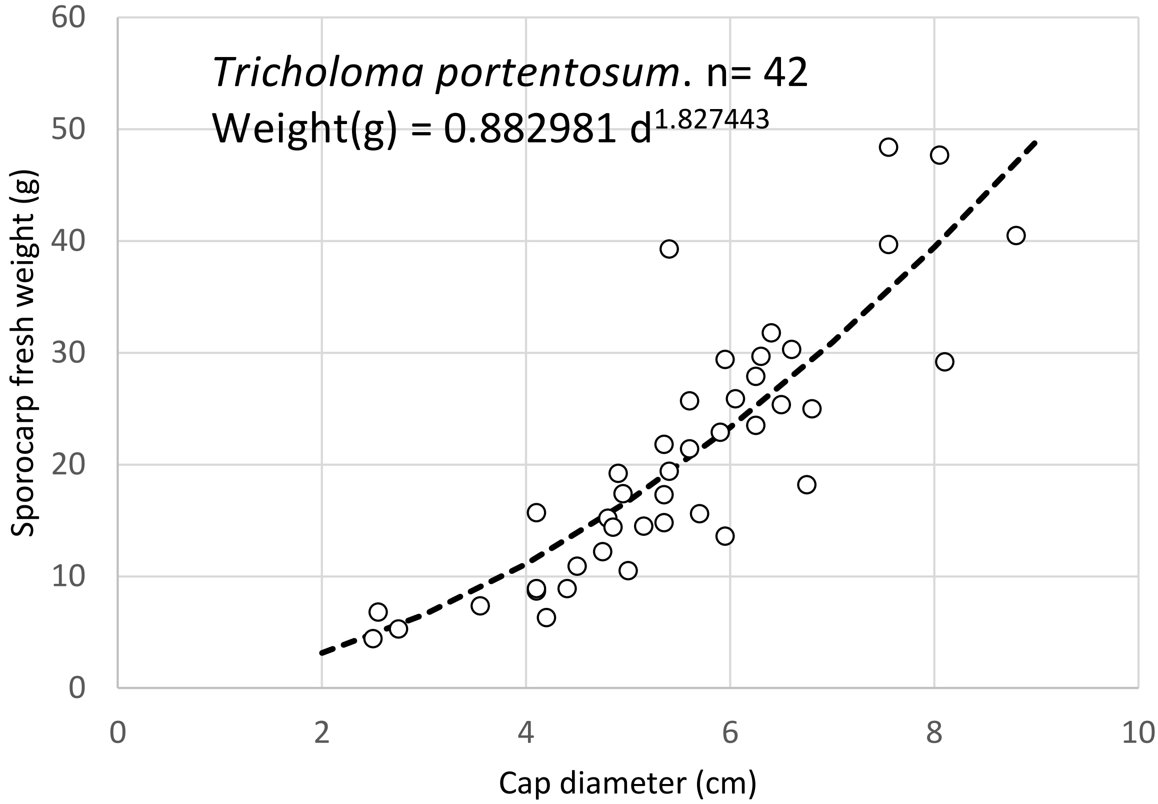

Figure 9. Plots of sporocarp weight versus cap diameter showing the fitted model for *Tricholoma portentosum*.

The results of the fitting of models are presented in Table 6. The strongest heteroscedasticity was observed in the *T. portentosum*, *I. badia*, *B. edulis* and *Lactarius quieticolor* data. Less heteroscedasticity was observed in the *S. luteus* and *H. repandum* data, thus showing a lower trend of cap weight variation as cap diameter increases. Precision was higher for *H. repandum*, *Lactarius quieticolor* and *S. luteus*, with RMSE values representing less than 30% of the average weight, whereas for *I. badia* and both boletes the relative RMSE was close to or higher than 50%. Most models indicated a slight trend for the sporocarp weight to be underestimated. The lowest accuracy was obtained in the model for *B. pinophilus*, with a positive BIAS of 6.5% of average weight, probably because of the variation in fresh weight of large sporocarps depending on rainfall and air humidity.

Table 6. Estimated parameters and model performance indicators for the nonlinear prediction of sporocarp weight from the cap diameter

Species	k in weight model	a_0	a_0 see	a_1	a_1 see	BIAS	RMSE
Boletus pinophilus	1.35	1.842544	0.3165	1.992456	0.0651	11.47	75.47
Hydnum repandum	0.81	0.971393	0.0790	1.697288	0.0442	-0.062	3.495
Lactarius quieticolor	1.50	0.359462	0.0429	2.266827	0.0563	0.3013	7.196
Imleria badia	1.51	0.742478	0.3399	2.084859	0.2064	1.054	23.98
Boletus edulis	1.59	5.536639	1.7628	1.499991	0.1316	1.017	66.38
Suillus luteus	1.10	0.470894	0.1021	2.339879	0.0972	0.969	11.56
Tricholoma portentosum	1.87	0.882981	0.3255	1.827443	0.1954	-0.094	5.931

a_0 and a_1: parameter estimates, "see": standard error of estimation for these parameters. BIAS: average error, and RMSE: root mean square error. k denotes the power function to model heterocedasticity.

The quality of boletes is closely related to the cap diameter, and the probability of obtaining the best quality decreases with the sporocarp development (Figures 3 and 4). Considering that all the sporocarps were classified in the three quality levels, the distribution of sporocarp number and fresh weight among qualities were determined, along with the average diameter of each quality for both boletes' species (Table 7). Almost half of the *B. pinophilus* productivity was classified as class 3, compared to only 31% for *B. edulis*. *B. edulis* was also more likely to maintain quality 1 and 2 levels for larger sizes than *B. pinophilus*.

Table 7. Sporocarp number, fresh weight and average diameter for the three qualities of boletes

Quality	*Boletus pinophilus*			*Boletus edulis*		
	Sporocarps (%)	Weight (%)	Average cap diameter (cm)	Sporocarps (%)	Weight (%)	Average cap diameter (cm)
Q1	40	24	6.0	36	30	6.2
Q2	22	27	9.6	33	39	9.3
Q3	38	49	11.5	31	31	9.8

4. DISCUSSION

4.1. Thinning and mushroom productivity

The mushroom productivity in the radiata pine stand under study was similar to, if not greater than, the average values reported for native pine species in Spain (Bonet et al., 2010; Alday et al., 2017). All of the species classified as marketable or edible in this study were ectomycorrhizal, and *C. prunulus* was probably also saprotrophic (Tedersoo et al., 2010), either restricted to conifers as host trees (*Lactarius quieticolor, T. portentosum, S. luteus*), with a strong preference for conifers (*I. badia, B. pinophilus, S. luteus*) or with a broader range of hosts including broadleaves and conifers (*B. edulis, H.*

repandum, Laccaria amethystina and *C. prunulus*). These species can be considered mesophilic rather than thermophilic (Sitta & Floriani, 2008), with an extended period of fruiting throughout the autumn, winter and even spring.

The mushroom productivity was best explained by the distance of the plot from the forest edge rather than as a result of the thinning regime. This may be a consequence of the advanced stage of development of the plantation, with the buffers being too small for the size of trees and stocking levels, and the position of the plot relative to the firebreaks being more important. Contrasting results on the effects of thinning on the fungal community have been reported and can probably be attributed to the diverse thinning types and weights, the fungal species studied and the period of time after thinning covered by each study (Egli et al., 2010).

In the present study, the most recent thinning intervention was applied 8 years before the first sampling plots were established for measuring mushroom productivity. Nonetheless, the *B. pinophilus* and *Lactarius quieticolor* productivity were lowest in the control plots. Productivity of *H. repandum* was good in the unthinned (control) plot, particularly for the Galician provenance, which was probably related to most of the control plots being located close to the forest edge (26.2 m on average, compared to 44.6 to 45.9 m for the thinning treatments).

Initial reductions in fruiting body yields have been observed, at least for some species such as *Cantharellus* (Pilz et al., 2006) in heavily thinned Douglas fir stands. These effects have been attributed to the initial soil disturbance derived from the forest operations. The effects lasted for 6 years in the aforementioned study (Pilz et al., 2006) and for four years in a mixed and dense old-growth stand in Central Europe (Egli et al., 2010)

If we consider the references related to plantations, Bonet et al. (2012) found immediate increases in the production of *L. deliciosus* after thinning of varying intensity (0-77% basal area removed) in a maritime pine (*Pinus pinaster* Ait.*)* stand. Kropp & Albee (1996) found that the total number of fruiting bodies was similar in thinned (with half of the trees removed) and undisturbed *Pinus contorta* Douglas ex Loudon stands, with increases in certain fungal species, particularly those of the *Suillus* and *Lactarius* genera, sustained for up to three years after thinning. Shaw et al. (2003) described the results of a four-year assessment after 50% thinning of a 12-years old Scots pine plantation, with little effect on the fungal community, although thinning increased counts of *Suillus bovinus* (L.) Roussel and other species.

Bonet et al. (2012) hypothesized that the effect of the temporal pattern of thinning on mushroom yield depends on the thinning intensity, with light thinning leading to an immediate positive response, whereas intensive thinning may lead to short-term negative effects after which the mushroom yield may recover and increase. Unfortunately, in the present study the first year of observation was 8 years after the second thinning was applied. This may explain the observations, along with the rather high values of basal area even in the more heavily thinning treatments (selective thinning show values greater than 40 m^2 ha^{-1}).

Setting target basal area levels is a reasonable criterion for establishing the optimal thinning regime for fungal production. The results obtained in Spain are somewhat variable, with values ranging from 20 m^2/ha for *Lactarius* (Bonet et al., 2008) to 30 m^2/ha for marketed mushrooms (Sánchez-González et al., 2019) and even 35-40 m^2 ha^{-1} for *B. edulis* growing in south-facing slopes in areas of Mediterranean climate (De Miguel et al., 2014). Tahvanainen et al. (2016) reported optimum levels of basal area for *B. edulis* production in spruce stands in Finland of 20 to 25 m^2 ha^{-1}, whereas the optimum was around 30 m^2 ha^{-1} for *Lactarius*. This approach may be useful, although in the plots of this study, the basal area in the different treatments converge to a narrow range (41-53 m^2 ha^{-1}), which is much higher than the proposed optimum.

In the present study, the positive effect of management on the emergence of ectomycorrhizal fruiting bodies is derived from the correlation of the stand management index and the total, commercial and pine bolete yield. This index has previously been used by Herrero et al. (2019) as an indicator of the forest management level for modelling mushroom productivity in a maritime pine stand. An active silviculture encompassing tree density reductions and brush control seems therefore essential to maintain a good fungal productivity.

The present study findings highlight the importance of wild edible mushroom productivity in planted pine forests, although the seedlings were not purposely mycorrhized in the nurseries. Nonetheless, *S. luteus* and the closely related *Lactarius* species have been used in controlled mycorrhization with successful sporocarp production (Savoie & Largetau, 2011).

4.2. Fungal inventory methods and development of fruiting bodies

The information on average sporocarp size and its variability may be of interest for anatomic description of the species and also for estimating yields by counting fruiting bodies in the inventories. Reports in the existing literature regarding fruiting body size are scarce. Martínez-Peña et al. (2012) reported the average weight of sporocarps collected between 1995 and 2004, with five species coinciding with those identified in the present study. The order of species size was similar, but *B. edulis* sporocarps were much smaller (76 g compared to 134.1g) in the *Pinus sylvestris* L. stands in the NE of the Iberian Peninsula. The same research group (Ortega-Martínez et al., 2011) studied the variation in size of *L. deliciosus* and *B. edulis* sporocarps depending on host tree age, with maximum sizes corresponding to the first age class (*P. sylvestris* less than 30 years old). As these authors pointed out, the average size of the sporocarps collected in the plots is directly related to the periodicity of inventory, which was also weekly in these studies.

Mycological inventories enable estimation of the yield and diversity of wild mushrooms in a given period of time and usually involve counting and weighing carpophores (Domínguez-Núñez & Oliet, 2023). Edible fungi are usually monitored by sampling permanent plots (sometimes fenced) or transects of minimum size 100 m^2 (Ortega-Martínez & Martínez-Peña, 2008). The methodology is limited when dealing with fruiting bodies of short lifespan, as the size would change according to the length of time that the fruit body remains sufficiently intact to distribute spores (Moore et al., 2008). Thus, the weight of fruiting bodies collected in the inventories will depend on the periodicity of sampling, as for long intervals some species would complete their cycle, thus reaching senescence, particularly if the fruiting bodies develop at high temperatures.

To overcome these problems and provide information on the fate of the fruiting bodies, Ortega-Martínez & Martínez-Peña (2008) proposed a sampling method involving the non-destructive observation of carpophore colonies and how they develop over time, with the number of missing specimens and their causal agents recorded weekly. This method enables the mycological yield to be classified into mature and immature carpophore production, harvested biomass, biomass consumed by livestock and biomass spoiled by parasites or trampling. This system provides more precise information about the productivity of carpophores and their sustainability but requires the use of allometric equations to estimate the weight of fruiting bodies.

The allometric equations developed in this study can also offer a tool to base the fungal inventory in only counting of fruiting bodies, if we consider an optimal cap diameter to harvest each species. The optimum size would be that maximizing the combination of the quality level of the carpophore and its weight. Caps larger than 8 cm for *B. pinophilus* would probably yield very low-quality classes, whereas the limit would be larger for *B. edulis* (Figures 3 and 4)

The information collected in this study can also provide reference levels for estimating average prices paid to mushroom pickers. Estimated averaged prices of 2 and 4 €/kg were assigned to the edible and marketable productions by Bonet et al. (2014), based on the published data of Martínez de Aragón et al. (2011) and Aldea et al. (2012), although the prices are known to vary depending not only on the species, but also particularly on the sporocarp quality. The FAO & WHO standards for edible fungus and fungus products establishes that “fresh edible fungi shall be healthy, i.e. not spoiled, practically clean, firm, undamaged, free, as far as possible, from maggot damage and shall possess the flavour and taste appropriate for the species” (FAO & WHO, 1981). In the case of boletes, small sporocarps with white tubes and pore surface are considered high quality and are also less likely to contain dipteran larvae, although the colour changes as the spores mature to a yellowish hue and finally become dark olive green (Sitta & Floriani, 2008).

The range of sizes found for the change of colour to yellow in the present study was 7 to 8 cm for both species of boletes. Harvesting only boletes with white hymenium could lead to removal of all the fruiting bodies before the spores are mature, as the ripening status can be determined in these species by a change in the colour of the hymenophore (Ortega-Martínez & Martínez-Peña, 2008). This consideration has led to the establishment of minimum sizes for collecting mushrooms in some European regional regulations, although Egli et al. (2006) demonstrated that weekly collection did not impair the future harvest, provided that trampling of the forest floor is minimised.

5. CONCLUSIONS

The average productivity of commercial mushroom species determined in this fast-growing radiata pine stand was 55.3 kg ha^{-1} year^{-1}, reaching 58.5 kg ha^{-1} year^{-1} when two edible non-commercial species were also considered. The stand under study was a mature, highly productive radiata pine plantation (mean annual increment in timber growth, 20.4 m^3 ha^{-1} year^{-1}), in which a thinning trial had been established, and the last thinning was performed 8 years before the mushroom inventories were started. Then, these mushroom productivity values can be considered representative of a healthy, mature plantation approaching rotation age. This can therefore be important for lengthening of the rotation, considering green retention during clearcutting or applying alternative regeneration felling.

The average sizes of sporocarps in terms of both weight and diameter decreased in the following order: *B. pinophilus* > *B. edulis* > *S. luteus* ≈ *I. badia* > *Lactarius quieticolor* > *T. portentosum* > *H. repandum*. Allometric relationships for these species are provided as a tool for future non-destructive inventory of fresh weight yield. Model precision was higher for *H. repandum*, *Lactarius quieticolor* and *S. luteus*, with most models tending to slightly underestimate the sporocarp weight. The *B. pinophilus* model was the least accurate, with a positive BIAS of 5.8% of average weight and a larger RMSE, probably because of the variation in fresh weight of large sporocarps according to rainfall and air humidity.

Overall, 51% of the collected fresh weight of *B. pinophilus* was classified in quality classes 1 or 2, whereas the corresponding figure for *B. edulis* was 69%. The sporocarp quality was closely related to the cap diameter, and the probability of finding fruiting bodies with white hymenium and firm flesh decreased with the sporocarp development. Quality classes 1 and 2 tended to be maintained for larger sizes of *B. edulis* than of *B. pinophilus*.

Supplementary information ↑

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Supplementary material

Not applicable.

Data availability

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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Authorship contribution statement

Javier Pereira-Espinel Plata: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing.

Roque Rodríguez-Soalleiro: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Julián Alonso-Díaz: Conceptualization, Data curation, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing.

Competing interests

The authors have declared that no competing interests exist.

Statement on the use of Artificial Intelligence

Not applicable.

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