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Modelling fuel loads of understorey vegetation and forest floor components in pine stands in NW Spain

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A R T I C L E I N F O

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Pinus pinaster
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A B S T R A C T

In this study, 310 destructively sampled plots were used to develop two equation systems for the three main pine species in NW Spain (*P. pinaster*; *P. radiata* and *P. sylvestris*): one for estimating loads of understorey fuel components by size and condition (live and dead) and another one for forest floor fuels. Additive systems of equations were simultaneously fitted for estimating fuel loads using overstorey, understorey and forest floor variables as regressors. The systems of equations included both the effect of pine species and the effect of understorey compositions dominated by ferns-brambles or by woody species, due to their obvious structural and physiological differences. In general, the goodness-of-fit statistics indicated that the estimates were reasonably robust and accurate for all of the fuel fractions. The best results were obtained for total understorey vegetation, total forest floor and raw humus fuel loads, with more than 76% of the observed variability explained, whereas the poorest results were obtained for coarse fuel loads of understory vegetation with a 53% of observed variability explained.

To reduce the overall costs associated with the field inventories necessary for operational use of the models, the additive systems were fitted again using only overstorey variables as potential regressors. Only relationships for fine (<6 mm) and total understorey vegetation and total forest floor fuel loads were obtained, indicating the complexity of the forest overstorey-understorey and overstorey-forest floor relationships. Nevertheless, these models explained around 52% of the observed variability.

Finally, equations estimating the total understorey vegetation and the total forest floor fuel loads based only on canopy cover were fitted. These models explained only 26%–32% of the observed variability; however, their main advantage is that although understorey vegetation in forested landscapes is largely invisible to remote sensing, canopy cover can be estimated with moderate accuracy, allowing for landscape-scale estimates of total fuel loads.

The equations represent an appreciable advance in understorey and forest floor fuel load assessment in the region and areas with similar characteristics and may be instrumental in generating fuel maps, fire management improvement and better C storage assessment by vegetation type, among many other uses.

1. Introduction

The understorey stratum, typically defined as all forest vegetation growing under an overstorey (Helms, 1998), plays an important role in the functioning of temperate forest ecosystems (Landuyt et al., 2019a). For example, it is involved in regulating numerous processes related to water and nutrient cycling, and it is responsible for a substantial part of the forest C stock (Gonzalez et al., 2013; Johnson et al., 2017) and net

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carbon and nitrogen fluxes in forests (Moore et al., 2007; Powell et al., 2008). It also affects the establishment and development of tree species at seedling stage as a result of facilitation and competition for essential resources (e.g., George and Bazzaz, 2014; Giuggiola et al., 2018; Helluy et al., 2021) or providing soil protection against erosion (see Levia and Frost, 2003 for a review). It also provides shelter and food for micro and macro fauna (e.g., Boch et al., 2013; Russell et al., 2017), and partly conditions litter quality and decomposition (Sigurdsson et al., 2005; Qiao et al., 2014), affecting the capacity of forest soils to sequester carbon. In addition, the understorey stratum is an important reservoir of biodiversity in temperate forests, containing, on average, more than 80% of vascular plant diversity (Gilliam, 2007). Diversity and species abundance are used as indicators of forest ecosystem health (Suchar and Crookston, 2010; Tkacz et al., 2013) and to evaluate the level of anthropogenic disturbance (Dale et al., 2002).

However, in addition to the beneficial effects of the understorey stratum on the persistence and stability of forest ecosystem, accumulation of fuels in the understorey is an important factor affecting the risk of wildfire (Fernandes and Rigolot, 2007; Coll et al., 2011). Greater accumulation of fuel load in the understorey can lead to a higher fireline intensity of surface fire (Byram, 1959; Fernandes et al., 2004, 2009), greater crown fire hazard (Agee and Skinner, 2005) and, therefore, undesirable ecological and economic consequences by increasing the probability of tree damage and mortality (Scott and Reinhardt, 2001). On the other hand, it also affects the effectiveness of fire suppression operations and the danger to firefighters (Scott and Reinhardt, 2001; Alexander and Cruz, 2011). Accumulation of fine fuels is particularly important as this fraction contributes most to fire spread, especially the dead fine fraction due to its lower moisture content and higher flammability during the maximum hazard season (Rothermel, 1972; Pyne et al., 1996; Madrigal et al., 2012). This scenario is frequent in the fire-prone landscape of pine stands in the NW of the Iberian Peninsula, where the overlapping of Mediterranean and Atlantic climatic influences cause periods of summer drought coexisting with high forest productivity. During the last decade (2012–2021), on average, more than 16,100 ha have been burned annually in this region, 41.36% of which were mainly pine and eucalyptus stands (Xunta de Galicia, 2022). The development of robust models for estimating understorey fuel loads that allow differentiation by fractions (fine and coarse fuels) and by physiological state (live and dead) in this type of stands is therefore important and necessary.

On the other hand, estimating the organic mass of the forest floor (including litter and duff) is also essential because of its fundamental role in the functioning of forest ecosystems, affecting water and nutrient cycles (e.g., Geddes and Dunkerley, 1999; Boeken and Orenstein, 2001; Vega et al., 2005), seedling regeneration and survival (e.g., Eckstein and Donath, 2005) and understorey herbaceous vegetation richness and composition (e.g., Casado et al., 2004). Moreover, the forest floor is critical in fire management and fire ecology, due to its flammability in a broad sense (Burton et al., 2021), as well as the central role played in soil burn severity generation through smouldering combustion (Vega et al., 2013) and substantial contribution to C emissions (Russell-Smith et al., 2009).

Overall, and as for the shrubland communities, two different approaches have been used to develop biomass estimation equations for understorey vegetation fuel load: the individual-level and the stand-level (area-based level) approaches. In the first approach, destructive sampling of individual plants is used and equations relating individual biomass to physical attributes such as basal diameter, height, crown area or phytomass are fitted. The biomass at a certain spatial scale (fuel load) is then obtained by aggregating the biomass of each individual. This method has been the most frequently used (e.g., Perala and Alban, 1993; Rue-Johns et al., 2021; Nolan et al., 2022) and is more appropriate for sparse understorey, typical of dense or overmature native stands.

In the stand-level approach, destructive sampling of all understorey vegetation is performed on sample plots of a certain area, and the allometric fuel load equations refer to the unit area, using understorey area-based attributes such as cover, mean height and phytovolume directly as predictors. This methodology has been considerably less well explored (e.g., Fernandes et al., 2002; Pimont et al., 2018) and could theoretically be more suitable for denser, relatively more homogeneous understories, such as in forests in NW Spain. In these stands, the understorey is frequently composed of multi-stemmed plants with intermingled crowns (Arellano et al., 2017), and measurement of individual plant variables is unfeasible or very costly and also requires the estimation of plant density for aggregation of individual biomass (Vega et al., 2022).

The influence of overstorey on understorey vegetation biomass is another factor to be considered in understorey fuel load modelling. At landscape-scale, understorey-overstorey interactions seem to be mainly dependent on abiotic restraints, disturbance regime, forest type and age, pre-closure vegetation type and species life-history traits, particularly shade and drought tolerance (e.g., Halpern and Lutz, 2013; Jin et al., 2022). At stand level, the overstorey structure and composition, which affect the availability of light, water, nutrients and space in the understorey, exert an overwhelming influence on the understorey vegetation (see reviews from Augusto et al., 2003 and Barbier et al., 2008), while the effects of overstorey on soil can also play a role (Landuyt et al., 2019a; López-Marcos et al., 2019).

Most studies assessing the effects of overstorey on understorey have focused on biodiversity attributes or structural parameters, such as cover or height, in different ecosystems (Coll et al., 2011; Fonseca and Duarte, 2017; Krebs et al., 2019; López-Marcos et al., 2019). Modelling the effects of overstorey on understorey biomass has received less attention (González-Hernández et al., 1998; Halpern and Lutz, 2013; Johnson et al., 2017; Jin et al., 2022), even though biomass is an important indicator of understorey functionality (Landuyt et al., 2019b). From the fire hazard standpoint, the scarcity of efforts in fuel load modelling at stand-level for understorey vegetation is remarkable (Fernandes et al., 2002, 2009; Castedo-Dorado et al., 2012; Parresol et al., 2012; Botequim et al., 2015; Mitsopoulos and Xanthopoulos, 2016). Furthermore, the scarcity of models breaking down load for size range fractions and vegetative state (live or dead) is even more remarkable, as there are almost no stand-level models, except for a very few ecosystems (Fernandes and Rego, 1998). Regarding forest floor, relationships between fuel loading and overstorey structural and compositional variables have been observed in some ecosystems (Hough and Albini, 1978; Lydersen et al., 2015), while the equivalent information for South European pine forests is scarce (Fernandes et al., 2002; López-Senespleda et al., 2021).

Accordingly, given the important modulating role of overstorey on understorey, it seems necessary to consider its potential influence and explore the possible explanatory ability of overstorey attributes in understorey fuel loading modelling. Consequently, the objectives of this study were to construct additive allometric biomass equations from biometric variables, using the stand-level approach and evaluating their performance to estimate the following: i) the total fuel load of the understorey vegetation, ii) the fuel component loads of the understorey vegetation (differentiated by size range and condition “live/dead”) and iii) the total fuel load of the soil organic layer and its components for the three most representative pine species in Galicia (NW Spain).

2. Material and methods

2.1. Study area and data used

The study was carried out in Galicia. This region occupies the NW Spain, between 41°40′ and 43°48′ N and 6°44′ and 9°18′ W. Pine forests cover more than 346,000 ha, which represents 24.4% of the forest area of the region (MARM, 2011). The dominant species are *Pinus pinaster* Ait. (≈217,000 ha), *Pinus radiata* D. Don (≈96,000 ha) and *Pinus sylvestris* L. (≈33,000 ha) in these stands. The climate of Galicia is transitional, with a larger western zone under temperate oceanic influence and the eastern side under Mediterranean dominance. The mean annual precipitation is 1,200 mm, varying spatially widely, between 500 and 1,800 mm, and the mean annual temperature is 13.3 °C, with a seasonal range of 8.5–19.0 °C (Martínez-Cortizas and Pérez-Alberti, 1999). The relief of the territory is quite irregular, with a predominance of mountains with moderate slopes.

The most common dominant vegetation in pine forest understorey is largely composed of evergreen woody species communities dominated by the genera *Ulex* and *Erica*. Other species of the genera *Calluna*, *Daboecia*, *Cistus*, *Pterospartum*, *Cytisus* and *Halimium* are commonly present in these communities, whereas others such as the deciduous *Vaccinium myrtillus* L. show a more localized occurrence. Non woody species, especially bracken fern (*Pteridium aquilinum* L.) and brambles (*Rubus* sp.), are very frequent and dominate large areas in the pine understorey, especially in humid and more productive sites, forming dense stands, alone or more frequently, mixed with woody species, forbs and grasses. Hereafter, the communities dominated by these species will be generically referred to as ferns-brambles or fern-bramble communities.

The data originate from a network of 346 temporary sampling plots established in pure and even-aged stands of the three most frequent pine species in the study area (*P. pinaster*, *P. radiata* and *P. sylvestris*), comprising a relatively wide quantitative range of the main attributes of these forests in Galicia (Fig. 1). Stands at early stages of development were not considered because in these cases there is symmetrical competition between trees and shrubs, so that the understorey load is often very similar to that found in treeless shrubs of the same formation. Thus, the final database consisted of data from 283 plots (180 of *P. pinaster*, 56 of *P. radiata* and 47 of *P. sylvestris* used to fit the systems of equations for estimating understorey shrub fuel loads and data from 310 plots (190 of *P. pinaster*, 67 of *P. radiata* and 53 of *P. sylvestris*) used to fit the systems of equations for estimating fuel loads of the soil organic layers, including in the latter case sample plots in forests without the understorey vegetation layer.

A circular sample plot of radius 8–15 m, depending on the stand density, was established in each selected stand, to include a minimum of 30 trees. For each tree, diameter at breast height (d) was measured to the nearest 0.1 cm, at two perpendicular angles, with a graduated caliper; total tree height (h) was measured to the nearest 0.1 m with a digital hypsometer and maximum crown diameter (D_c) was measured to the nearest 0.01 m with a tape.

Stand density (N, trees·ha^{-1}), stand basal area (G, m^2·ha^{-1}), mean diameter ($\bar{d}$, cm), mean height ($\bar{h}$, m), canopy cover (CC, %), mean distance between trees, considering a theoretical square grid ($\delta = 100/\sqrt{N}$, m), relative spacing index, defined as the ratio between mean distance between trees and mean height (RSI $= \delta/\bar{h}$) and stand density index (SDI $= N \times (25/\bar{d})^{-1.605}$, trees·ha^{-1}) were directly calculated for the three field-measured tree variables. Additionally, canopy bulk density (CBD, kg·m^{-3}) was obtained using the equations proposed for the three pine species in Galicia by Fernández-Alonso et al. (2013) with G and N as regressors.

The understorey fuels were destructively sampled by randomly selecting two perpendicular diameters in the sampling plot and placing four sampling squares in the centre of each radius. The side of the sampling square was 1 m for herbaceous or woody vegetation lower than 0.5 m in height and 2 m for heights greater than 0.5 m.

A sampling transect consisting of the sampling square perimeter plus one diagonal was delimited. The horizontal lengths of the intercepted shrub species (cm) were measured along this linear transect, to estimate the linear shrub cover by species according to the method proposed by Canfield (1941). Total shrub height (cm) was also measured every 50 cm. These measurements were used to calculate total shrub cover (Cov$_{Shr}$, %) and mean shrub height ($\overline{h}_{Shr}$, cm).

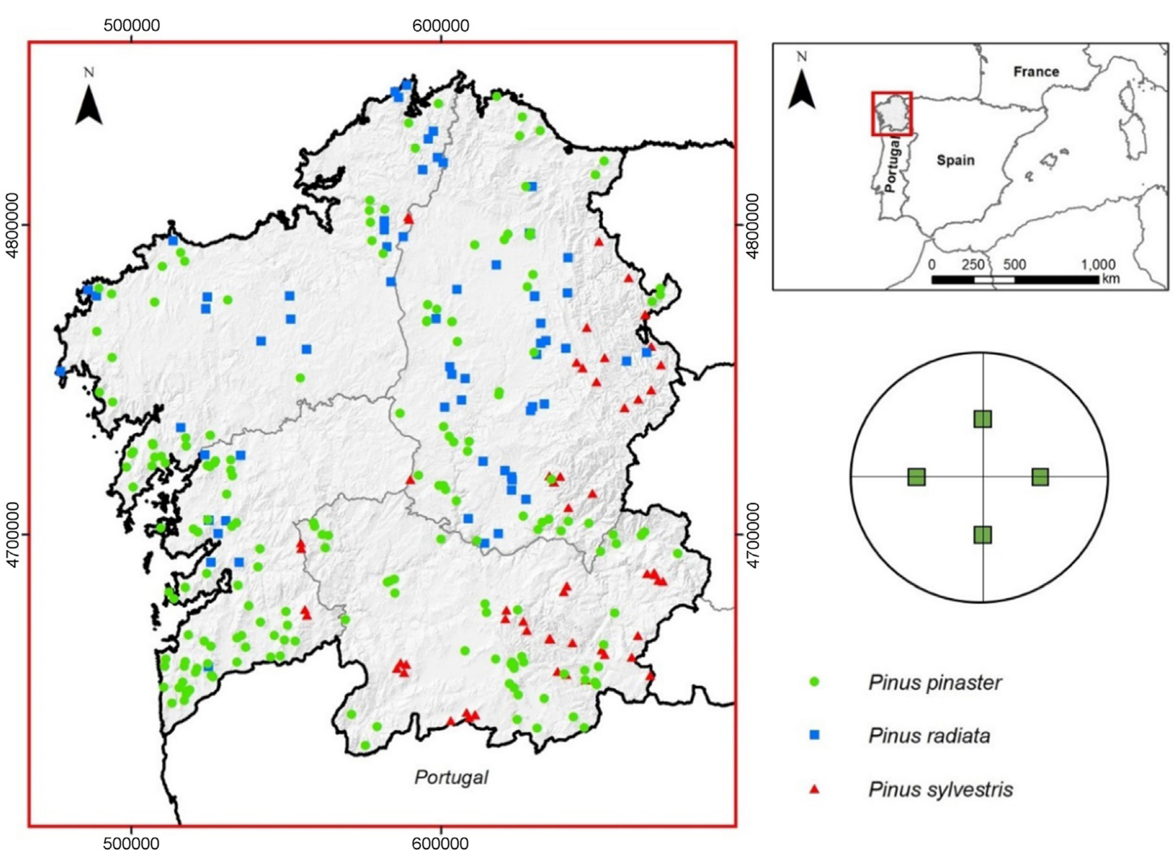

Fig. 1. Geographical location of the 310 inventory plots in Galicia (left). Coordinate system ETRS89, Zone 29 N (EPGS: 25829). Layout of inventory plot showing transects and location of four destructive sampling subplots (quadrats m, in green) in each inventory plot (middle right). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

All of the shrub layer in the vertical projection of the sampling square area were carefully harvested at ground level and placed in bags, which were labelled appropriately and transported to the laboratory. After removal of the shrub layer, the woody debris was also sampled, although the information obtained was not included in this study because it was only observed in a limited number of sample plots. Soil organic layers (L (fresh litter), F (partially decomposed litter) and H (raw humus)) were then inventoried, separating each from top to bottom. The depth of the L and F layers was measured at ten points along the perimeter and diagonal of the sampling square (mm), and these fractions were collected separately. The next step was to randomly locate a 30 cm × 30 cm wood frame inside the sampling square and extract the H layer until the mineral soil is reached. Once extracted, the H depth (mm) was measured at 10 points along the perimeter of the wood frame. The measurements of the thickness of each layer were averaged to determine the average depth of each layer and of the total ($\overline{d_{LFH}}$, cm). All of this material was also placed in labelled bags for transfer to the laboratory.

Once in the laboratory, the shrub samples were classified into three size ranges according to their thickness: fine fuels (diameter <0.6 cm, hereafter G1), medium fuels (0.6 cm ≤ diameter <2.5 cm, hereafter G2) and coarse fuels (2.5 cm ≤ diameter <7.5 cm, hereafter G3) by using a go-no go gauge (Brown et al., 1982). The fine fuels were further subdivided by condition (live and dead), determined by visual inspection. The size categories facilitate the construction of custom-built fuel models for predicting fire behaviour (Burgan and Rothermel, 1984; Finney, 1998; Scott and Burgan, 2005). The classified material was weighed and dried in forced air-drying chambers (105 °C for 24 h for fine fuels and 48 h for coarse fuels) for determination of the dry biomass of each fraction. For the duff organic layer, samples were oven-dried for 48 h to 105 °C and one oven-dried subsample of layer H was combusted in a muffle furnace at 550 °C for 4 h (Federer, 1982) to determine the loss on ignition. This value was applied to the oven-dried duff samples mass to obtain an H layer load value free of mineral soil contamination.

Thus, eight different loads of the respective biomass fractions were computed. The five loads related to the shrub stratum were $W_{Shr\_G1\_dead}$ = dead fine shrub load, $W_{Shr\_G1\_live}$ = live fine shrub load, W_{Shr_G1} = fine shrub load (dead + live), W_{Shr_G23} = coarse shrub load and W_{Shr} = total shrub load or AGB at stand-level ($W_{Shr\_G1} + W_{Shr\_G23}$). Biomass fractions G2 and G3 were grouped to prevent loss of data, as fraction G3 is infrequent in many of the communities. In addition, the following three loads corresponding to the soil organic layer were calculated: W_{LFH} = total soil organic layers load, W_{LF} = L and F layers load and W_H = H layer load. The whole sampling process is described in greater detail in Vega et al. (2022) and Arellano et al. (2017).

The mean value and standard deviation of the main overstorey and understorey variables of the 283 sample plots used to fit the systems of equations for estimating understorey shrub fuel loads are shown in Table 1. We distinguished between understorey formations dominated by ferns-brambles ("Pa") and by woody species ("shrubs") due to their obvious structural and physiological differences. The mean value and standard deviation of the main overstorey, understorey and forest floor layer variables of the 310 sample plots used to fit the systems of equations to estimate fuel loads of the soil organic layers are shown in Table 2. As previously mentioned, this database included sample plots with absence of understorey ("Au").

2.2. Statistical analysis

2.2.1. Models for estimating shrub fuel loads

As the sample was not large enough to fit specific models for each understorey community within each of the three pine species, we initially fitted a single system of estimating equations for the total data set. In a first step, allometric models ($y = \alpha_0 X_i^{\alpha_i}$) were fitted to estimate the biomass loads for each of the fuel fractions considered separately. The allometric models were linearized using logarithmic transformations, and the stepwise method was used to select the best set of independent variables for each fraction (X_i) considering both overstorey variables ($\overline{d}$, $\overline{h}$, N, G, CC_{Bliss}, CBD, RSI and SDI) and understorey variables ($\overline{h_{Shr}}$ and Cov_{Shr_Bliss}). The variables CC_{Bliss} and Cov_{Shr_Bliss} were obtained by arcsine-square root transformation of the canopy cover (CC, %) and total shrub cover (Cov_{Shr}, %), respectively, to stabilize the variance and improve normality (Bliss, 1938).

The proposed allometric equations must satisfy the additivity property, i.e., the sum of the biomasses estimated for each fraction separately

Table 1
Mean value and standard deviation of the main overstorey and understorey variables distinguished by pine species and by dominant understorey species (Pa, fern-bramble communities; shrubs, woody species; *n*, number of sample plots).

Variable	Statistic	Pinus pinaster		Pinus radiata		Pinus sylvestris	
		Pa	shrubs	Pa	shrubs	Pa	shrubs
		$n = 68$	$n = 112$	$n = 24$	$n = 32$	$n = 14$	$n = 33$
$\overline{d}$ (cm)	Mean	22.96	18.44	23.43	20.34	23.05	18.70
	St. dev.	4.96	4.69	5.72	8.35	3.76	5.00
$\overline{h}$ (m)	Mean	17.16	12.25	17.49	14.14	16.16	12.28
	St. dev.	4.01	3.43	4.84	5.78	2.39	2.71
N (stems·ha^{-1})	Mean	997.95	1455.00	884.99	849.04	1080.93	998.70
	St. dev.	598.21	1071.07	321.87	420.15	382.27	352.27
G (m^2·ha^{-1})	Mean	39.96	36.55	41.74	37.47	43.43	38.91
	St. dev.	10.48	10.67	19.30	18.22	9.71	15.55
CC (%)	Mean	65.89	63.92	63.98	49.39	70.93	58.95
	St. dev.	8.90	11.03	12.85	17.08	5.22	11.18
Cov_{Shr} (%)	Mean	72.59	61.75	74.46	82.84	77.86	75.59
	St. dev.	21.17	28.79	23.52	21.32	9.83	19.54
$\overline{h_{Shr}}$ (cm)	Mean	65.93	77.47	60.99	75.62	62.35	65.10
	St. dev.	21.42	38.44	30.25	39.77	15.73	20.74
W_{Shr} (kg·m^{-2})	Mean	0.2666	0.9042	0.4428	1.6486	0.3874	1.4255
	St. dev.	0.1597	0.6079	0.3363	1.0136	0.1465	0.8633
W_{Shr_G23} (kg·m^{-2})	Mean	0.0580	0.2954	0.0898	0.4915	0.1114	0.5108
	St. dev.	0.0554	0.3103	0.0778	0.3561	0.0692	0.3292
W_{Shr_G1} (kg·m^{-2})	Mean	0.2085	0.6089	0.3530	1.1571	0.2759	0.9148
	St. dev.	0.1407	0.4080	0.3348	0.7496	0.0892	0.6094
$W_{Shr\_G1\_dead}$ (kg·m^{-2})	Mean	0.1221	0.3794	0.2291	0.7240	0.1944	0.5466
	St. dev.	0.0751	0.2681	0.2878	0.5101	0.0603	0.3628
$W_{Shr\_G1\_live}$ (kg·m^{-2})	Mean	0.0864	0.2295	0.1238	0.4331	0.0815	0.3682
	St. dev.	0.1204	0.1801	0.1266	0.2695	0.0448	0.2595

Table 2
Mean value and standard deviation of the main overstorey, understorey and forest floor variables distinguished by pine species and by absence of understorey ("Au") or dominant communities (Pa, ferns-brambles; shrubs, woody species; *n*, number of sample plots).

Variable	Statistic	*Pinus pinaster*			*Pinus radiata*			*Pinus sylvestris*		
		Au	Pa	shrubs	Au	Pa	Shrubs	Au	Pa	shrubs
		$n = 20$	$n = 64$	$n = 106$	$n = 14$	$n = 22$	$n = 31$	$n = 6$	$n = 14$	$n = 33$
$\bar{d}$ (cm)	Mean	22.14	23.06	18.54	24.52	24.21	20.60	23.07	23.05	18.70
	St. dev.	5.41	4.99	4.69	8.38	5.14	8.22	4.07	3.63	4.92
$\bar{h}$ (m)	Mean	16.34	17.47	12.34	16.09	18.34	14.27	14.94	16.16	12.28
	St. dev.	3.84	3.75	3.43	2.82	3.96	5.74	3.92	2.31	2.67
N (stems·ha^{-1})	Mean	1389.42	1011.56	1480.54	829.88	910.03	866.33	1630.33	1080.93	998.70
	St. dev.	1088.04	609.04	1087.52	451.92	315.87	408.61	899.77	368.37	346.89
G (m^2·ha^{-1})	Mean	41.72	40.34	36.92	41.21	44.50	38.46	49.61	43.43	38.91
	St. dev.	13.39	10.01	10.51	12.83	17.26	17.34	15.94	9.35	15.32
CC (%)	Mean	62.11	65.77	64.57	62.14	65.98	50.40	62.97	70.93	58.95
	St. dev.	13.26	8.89	10.47	16.64	10.21	16.09	21.00	5.03	11.01
Cov_{Shr} (%)	Mean	–	71.41	61.59	–	72.76	82.60	–	77.86	75.59
	St. dev.	–	20.91	28.94	–	23.32	21.28	–	9.47	19.24
$\overline{h_{Shr}}$ (cm)	Mean	–	66.60	78.28	–	63.65	73.16	–	62.35	65.10
	St. dev.	–	20.74	39.02	–	29.48	37.25	–	15.16	20.42
$\overline{d_{LFH}}$ (cm)	Mean	8.61	8.56	7.83	6.57	9.39	8.12	10.27	11.58	9.69
	St. dev.	2.15	3.51	2.97	2.07	2.91	3.30	2.14	1.97	3.28
$\overline{d_{LF}}$ (cm)	Mean	4.45	4.60	4.37	3.18	4.47	3.71	4.57	4.01	3.70
	St. dev.	2.27	2.51	2.26	1.66	1.49	2.11	0.83	1.16	1.59
$\overline{d_{H}}$ (cm)	Mean	4.16	3.96	3.47	3.39	4.92	4.41	5.70	7.56	5.99
	St. dev.	1.44	1.94	1.54	1.53	2.02	2.06	2.27	1.65	2.18
W_{LFH} (kg·m^{-2})	Mean	3.27	3.38	3.21	3.01	4.09	3.38	5.44	5.86	4.97
	St. dev.	0.97	1.05	0.93	0.86	1.43	1.64	1.31	1.17	2.00
W_{LF} (kg·m^{-2})	Mean	1.19	1.19	1.21	0.98	1.34	1.10	1.18	1.27	1.19
	St. dev.	0.50	0.55	0.44	0.30	0.47	0.60	0.23	0.30	0.59
W_{H} (kg·m^{-2})	Mean	2.08	2.19	2.00	2.03	2.75	2.29	4.26	4.58	3.79
	St. dev.	0.73	0.82	0.69	0.83	1.25	1.25	1.46	1.14	1.63

must equal the biomass estimated by the total load equation; the same is true for the fine load fractions relative to the total fine load. To ensure additivity, the system composed of five equations was fitted simultaneously and consists of the following equations:

1) An allometric equation to estimate the total understorey vegetation fuel load ($\widehat{W_{Shr}}$)

$$\widehat{W_{Shr}} = a_0 X_i^{a_i} \quad (1)$$

2) Two equations discriminated between fine ($\widehat{W_{Shr\_G1}}$) and coarse fuel loads ($\widehat{W_{Shr\_G23}}$) by disaggregating equation (1):

$$\widehat{W_{Shr\_G23}} = \exp[b_{0_{G23}} + b_{i_{G23}} \log(X_i)]$$

$$\widehat{W_{Shr\_G1}} = \exp[b_{0_{G1}} + b_{i_{G1}} \log(X_i)]$$

$$\frac{\widehat{W_{Shr\_G23}}}{\widehat{W_{Shr}}} = \frac{\widehat{W_{Shr\_G23}}}{(\widehat{W_{Shr\_G23}} + \widehat{W_{Shr\_G1}})} = \frac{1}{1 + (\widehat{W_{Shr\_G1}}/\widehat{W_{Shr\_G23}})}$$

The equation for estimating the coarse fuel loads was then obtained as follows:

$$\widehat{W_{Shr\_G23}} = \frac{\widehat{W_{Shr}}}{1 + \exp[b_0 + b_i \log(X_i)]} \quad (2)$$

with $b_i = b_{iG1} - b_{iG23}$;

and, therefore, the equation for estimating the fine fuel load was as follows:

$$\widehat{W_{Shr\_G1}} = \widehat{W_{Shr}} - \widehat{W_{Shr\_G23}} = \frac{\widehat{W_{Shr}} \exp[b_0 + b_i \log(X_i)]}{1 + \exp[b_0 + b_i \log(X_i)]} \quad (3)$$

3) Finally, two equations discriminated between dead fine ($\widehat{W_{Shr\_G1\_dead}}$) and live fine fuel loads ($\widehat{W_{Shr\_G1\_live}}$) loads by disaggregating equation (3):

$$\widehat{W_{Shr\_G1\_dead}} = \exp\left[c_{0_{G1\_dead}} + c_{i_{G1\_dead}} \log(X_i)\right]$$

$$\widehat{W_{Shr\_G1\_live}} = \exp\left[c_{0_{G1\_live}} + d_{i_{G1\_live}} \log(X_i)\right]$$

$$\frac{\widehat{W_{Shr\_G1\_dead}}}{\widehat{W_{Shr\_G1}}} = \frac{\widehat{W_{Shr\_G1\_dead}}}{(\widehat{W_{Shr\_G1\_dead}} + \widehat{W_{Shr\_G1\_live}})} = \frac{1}{1 + (\widehat{W_{Shr\_G1\_live}}/\widehat{W_{Shr\_G1\_dead}})}$$

The equation for estimating the fine dead fuel loads was then obtained:

$$\widehat{W_{Shr\_G1\_dead}} = \frac{\widehat{W_{Shr\_G1}}}{1 + \exp[c_0 + c_i \log(X_i)]} \quad (4)$$

with $c_i = c_{iG1\_live} - c_{iG1\_dead}$;

and the equation for estimating the fine live fuel load was as follows:

$$\widehat{W_{Shr\_G1\_live}} = \widehat{W_{Shr\_G1}} - \widehat{W_{Shr\_G1\_dead}} = \frac{\widehat{W_{Shr\_G1}} \exp[c_0 + c_i \log(X_i)]}{1 + \exp[c_0 + c_i \log(X_i)]} \quad (5)$$

Due to the particular biology of fern-bramble communities (Pa) and their wide structural and physiological variability throughout the year, the effect of these species on the system of equations was analyzed by expanding the α_0 parameters (a_0, b_0 and c_0) by including a new parameter affected by a dummy variable (I_{Pa}) taking the value 1 for ferns-brambles and 0 otherwise. Likewise, to assess the effect of the different dominant pine species, another two parameters were included with their associated dummy variables I_{Ps} and I_{Pr}, which take values of 1 if the dominant pine species is *P. sylvestris* (Ps) or *P. radiata* (Pr), respectively and 0 otherwise. Therefore, the parameters α_0 were finally established as follows:

$$\alpha_0 = \alpha_{00} + \alpha_{Pa} I_{Pa} + \alpha_{Ps} I_{Ps} + \alpha_{Pr} I_{Pr}$$

2.2.2. Models for estimating forest floor layer loads

A system of three equations was developed for estimating the total forest floor loads, the fresh and partially decomposed litter and the raw humus layers (W_{LFH}, W_{LF} and W_H). This system was fitted independently from the system of equations to estimate the fuel loads of the understorey vegetation layer due to differences in the database used as there were sample plots without the understorey vegetation layer but with the presence of litter and duff layers.

A similar approach was used and the system consists of a first equation for estimating the total forest floor load (L, F and H layers, $\widehat{W_{LFH}}$):

$$\widehat{W_{LFH}} = d_0 X_i^{d_i} \tag{6}$$

Another two equations were obtained by disaggregating the previous one to produce the fuel loads of the L and F layers ($\widehat{W_{LF}}$) and, on the other hand, the fuel load of the H layer ($\widehat{W_H}$):

$$\widehat{W_{LF}} = \exp\left[f_{0_{LF}} + f_{i_{LF}} \log(X_i)\right]$$

$$\widehat{W_H} = \exp\left[f_{0_H} + f_{i_H} \log(X_i)\right]$$

$$\frac{\widehat{W_{LF}}}{\widehat{W_{LFH}}} = \frac{\widehat{W_{LF}}}{(\widehat{W_{LF}} + \widehat{W_H})} = \frac{1}{1 + (\widehat{W_H}/\widehat{W_{LF}})}$$

Therefore, the equation for estimating the fuel load of the L and F layers was obtained as follows:

$$\widehat{W_{LF}} = \frac{\widehat{W_{LFH}}}{1 + \exp[f_0 + f_i \log(X_i)]} \tag{7}$$

with $f_i = f_{iH} - f_{iLF}$.

Accordingly, the equation for estimating the fuel load of the H layer was expressed as follows:

$$\widehat{W_H} = \widehat{W_{LFH}} - \widehat{W_{LF}} = \frac{\widehat{W_{LFH}} \exp[f_0 + f_i \log(X_i)]}{1 + \exp[f_0 + f_i \log(X_i)]} \tag{8}$$

In this system of equations, the independent variables (X_i) analyzed include, in addition to all of those mentioned for the system to estimate understorey vegetation fuel loads, the total depth of the forest floor and the depth of LF and H layers ($\overline{d_{LFH}}$, $\overline{d_{LF}}$ and $\overline{d_H}$).

Again, in this system, the effect of the dominance of fern-bramble communities on the understorey and the different pine species was analyzed by expanding the α_0 parameters (d_0 and f_0) by including dummy variables (I_{Pa}, I_{Ps} and I_{Pr}).

Moreover, we explored the possibility of providing systems that enable estimation of the fuel loads without sampling understorey or forest floor characteristics. Thus, the same two equation systems described above were fitted using only overstorey attributes as regressors (X_i).

The four systems were fitted using the generalized method of moments (GMM) of the MODEL procedure of the SAS/ETS program (SAS Institute Inc, 2004). This approach yields efficient estimators of the parameters in the presence of heteroscedastic errors. To evaluate the presence of multicollinearity, the condition number was used and, following the criterion of Myers (1990), variables with values greater than $\sqrt{1000}$ were excluded from the models.

Finally, to evaluate the accuracy of the estimates of the fitted models, two goodness-of-fit statistics were used: the model efficiency (ME), calculated as the square of the correlation coefficient between the observed and predicted values, and the root mean squared error (RMSE).

$$\mathrm{ME} = \rho^2_{y_i \widehat{y_i}} \tag{9}$$

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n} (Y_i - \widehat{Y}_i)^2}{n-1}} \tag{10}$$

where Y_i and $\widehat{Y}_i$ are the observed and the predicted value of the dependent variable, respectively, and n is the number of sample plots used to fit the models.

3. Results

3.1. Equations based on overstorey, understorey and forest floor variables

The mathematical expressions of the models finally fitted for the shrub fuel loads and for the forest floor fuel loads as well as with the values of the goodness-of-fit statistics are shown in Table 3. All parameters were found to be significant ($\alpha = 0.05$), and no multicollinearity problems were observed.

Regarding the system of equations for estimating understorey fuel loads, the independent variables finally included in the models were the mean shrub height ($\overline{h_{Shr}}$, cm), the transformed total shrub cover (Cov_{Shr_Bliss}) and the stand density index (SDI). In addition, in the allometric model for estimating the total understorey fuel load (Eq. 1), the effects of the presence of ferns-brambles as the dominant community in the understorey and *P. sylvestris* and *P. radiata* as dominant species in the overstorey were significant. The dominance of ferns-brambles resulted in a reduction in the total fuel load relative to woody shrubs, and the dominance of *P. sylvestris* and *P. radiata* implied an increase in the total fuel load relative to *P. pinaster*. Moreover, these effects were also significant in parameter b_0, affecting the disaggregation of the total understorey fuel load in group 2–3 and group 1 fuel loads (Eqs. 2 and 3), respectively), although in this case there were no significant differences between stands with *P. radiata* and *P. pinaster* dominance. In the latter case, the dominance of ferns-brambles in the understorey resulted in an increase in the ratio of fine fuels (W_{Shr_G1}/W_{Shr}) relative to woody shrub types, and the dominance of *P. sylvestris* implied a reduction in the ratio of fine fuels relative to the other two pine species. There were no significant differences between shrub types or between pine species in the ratio of dead fine fuel ($W_{Shr\_G1\_dead}/W_{Shr\_G1}$), with the stand density index being the only variable apparently influencing this ratio.

As previously mentioned, the particular structural and physiological characteristics of the ferns-brambles and their variations throughout the year require measurement of the input variables ($\overline{h_{Shr}}$ and Cov_{Shr_Bliss}) when the ferns are fully developed and the fronds are alive.

On the other hand, in the case of the system for estimating forest floor layer loads, the independent variables finally included in the models were the total depth of the L, F and H layers ($\overline{d_{LFH}}$), the depth of the L and F layers considered together ($\overline{d_{LF}}$) and the stand basal area (G). In this case, the parameter associated with the dummy variable analysing the effect of *P. sylvestris* as dominant tree species was the only significant parameter affecting both d_0 and f_0 parameters, increasing the fuel loads relative to *P. pinaster* and *P. radiata*.

Figs. 2 and 3 show the plots of observed versus predicted values obtained with the fitted equation systems for understorey vegetation and forest floor fuel loads, respectively.

3.2. Equations only based on overstorey variables

The results obtained in the simultaneous fitting of the understorey and forest floor fuel load equation systems including only overstorey variables as regressors yielded estimates for the extreme values of the dependent variable with a strong tendency towards its mean, precluding obtaining robust and additive models for both systems of equations. Therefore, only allometric models were proposed for those fuel fractions showing acceptable goodness-of-fit statistics and good graphical representations of studentized residuals versus predicted values and of

Table 3
Mathematical expressions of fitted models and values of goodness-of-fit statistics with overstorey, understorey and forest floor variables considered potentially independent variables.

Eq.	Mathematical expression	ME	RMSE ($kg \cdot m^{-2}$)
Equation system for estimating understorey fuel loads based on overstorey and understorey variables			
1	$\widehat{W_{Shr}} = (0.7733 - 0.5769 I_{Pa} + 0.2147 I_{Ps} + 0.1236 I_{Pr}) \overline{h}_{Shr}^{0.5479} Cov_{Shr\_Bliss}^{1.1911} SDI^{-0.3273}$	0.7647	0.3691
2	$\widehat{W_{Shr\_G23}} = \frac{\widehat{W_{Shr}}}{1 + \exp[2.0276 + 0.4313 I_{Pa} - 0.2921 I_{Ps} - 0.3049 \log(\overline{h}_{Shr}) + 0.5108 \log(Cov_{Shr\_Bliss})]}$	0.5268	0.2108
3	$\widehat{W_{Shr\_G1}} = \frac{\widehat{W_{Shr}} \exp[2.0276 + 0.4313 I_{Pa} - 0.2921 I_{Ps} - 0.3049 \log(\overline{h}_{Shr}) + 0.5108 \log(Cov_{Shr\_Bliss})]}{1 + \exp[2.0276 + 0.4313 I_{Pa} - 0.2921 I_{Ps} - 0.3049 \log(\overline{h}_{Shr}) + 0.5108 \log(Cov_{Shr\_Bliss})]}$	0.7322	0.2736
4	$\widehat{W_{Shr\_G1\_dead}} = \frac{\widehat{W_{Shr\_G1}}}{1 + \exp[0.0740 \log(SDI)]}$	0.6073	0.1365
5	$\widehat{W_{Shr\_G1\_live}} = \frac{\widehat{W_{Shr\_G1}} \exp[0.0740 \log(SDI)]}{1 + \exp[0.0740 \log(SDI)]}$	0.6806	0.1939
Equation system for estimating forest floor fuel loads based on overstorey and forest floor variables			
Eq.	**Mathematical expression**	**ME**	**RMSE ($kg \cdot m^{-2}$)**
6	$\widehat{W_{LFH}} = (0.3825 + 0.0918 I_{Ps}) \overline{d_{LFH}}^{0.7102} G^{0.2042}$	0.7829	0.7182
7	$\widehat{W_{LF}} = \frac{\widehat{W_{LFH}}}{1 + \exp\left[-0.8259 + 0.3625 I_{Ps} + 0.2494 \log(G) - 0.7579 \log\left(\frac{\overline{d_{LF}}}{\overline{d_{LFH}}}\right)\right]}$	0.5465	0.3480
8	$\widehat{W_H} = \frac{\widehat{W_{LFH}} \exp[-0.8259 + 0.3625 I_{Ps} + 0.2494 \log(G) - 0.7579 \log(\overline{d_{LF}}/\overline{d_{LFH}})]}{1 + \exp[-0.8259 + 0.3625 I_{Ps} + 0.2494 \log(G) - 0.7579 \log(\overline{d_{LF}}/\overline{d_{LFH}})]}$	0.7819	0.6092

observed values versus predicted values when the equations were fitted independently. Finally, models were obtained for the total understorey fuel load ($\widehat{W_{Shr}}$), for the fine understorey load ($\widehat{W_{Shr\_G1}}$) and for the total forest floor layer fuel load ($\widehat{W_{LFH}}$) (see Table 4). All parameters were significant ($\alpha = 0.05$) and no multicollinearity problems were observed. However, heteroscedasticity was observed in the equation for estimating the total litter and duff layer fuel load and, therefore, a weighting factor of $1/G^{0.4052}$ was included to correct this, according to the method proposed by Harvey (1976).

In the understorey loading equations, the independent variables included in the models were the transformed canopy cover fraction (CC_{Bliss}), stand basal area (G) and stand density index (SDI). Parameters a_0 and b_0 were again expanded to include significant parameters addressing the effect of ferns-brambles as the dominant community of the understorey vegetation and the effect of the dominance of different pine species in the canopy. The dominance of ferns-brambles resulted in a reduction of the estimated $\widehat{W_{Shr}}$ and $\widehat{W_{Shr\_G1}}$ fuel loads, whereas the dominance of *P. radiata* and *P. sylvestris* resulted in an increment in $\widehat{W_{Shr}}$ fuel load relative to *P. pinaster*.

Regarding the total litter and duff load equation, the only independent variable was the stand basal area (G) and the parameter addressing the effect of *P. sylvestris* as the dominant species was the only significant one, resulting in an increase in the total forest floor load relative to the other two pine species. Fig. 4 shows the plots of observed versus predicted values obtained with the 3 fitted equations.

Finally, another two equations were fitted independently to estimate the total and fine fuel load of the understorey (W_{Shr} and W_{Shr_G1}) as a function only of the overstorey variable that yielded the best goodness-of-fit statistics, which in both cases was the transformed canopy cover fraction (CC_{Bliss}), for both understorey dominated by ferns-brambles or woody species. These equations can therefore be used for landscape-scale estimates in remote sensing that can accurately estimate canopy cover (LiDAR, UAV or high-resolution satellite imagery). All parameters were significant ($\alpha = 0.05$) and in both cases the effect of *P. radiata* and *P. sylvestris* dominance resulted in a significant increase in fuel loads (Table 5).

4. Discussion

The loads of total understorey vegetation (W_{Shr}) and forest floor (W_{LFH}) fuel layers observed in this study are within the range of values obtained for understorey of these pine species under site conditions characterized by similar climatic, physiographical and edaphic conditions to those in the study area (e.g., González-Hernández et al., 1998; Vega, 2001; Fernandes et al., 2002, 2009; Fernandes and Rigolot, 2007; Cruz et al., 2011; Castedo-Dorado et al., 2012; Botequim et al., 2015; Arellano et al., 2017).

The mean value of W_{Shr} (0.831 $kg \cdot m^{-2}$) was consistently higher than observed in most of the equivalent pine forests in temperate or boreal climate (e.g., Fernandes et al., 2004; Merilä et al., 2014) and comparable to productive forest from the South-East of north America (Hough and Albini, 1978; Parresol et al., 2012) and cold temperate forest in China (Jin et al., 2022).

The high live biomass of the understorey vegetation in pine stands in north-western Spain, despite the restrictive values of overstorey attributes (Table 1), suggests a considerable potential for competitive endurance of the understorey vegetation. Several factors may affect the outcome. First, these relatively young stands originated from afforestation on land with a long history of human use and covered by robust and dense shrub communities. Hence, insufficient time has probably passed for a balance to be reached between the biomass of the two layers of vegetation involved, as the understorey response can typically lag considerably after disturbance (Kerns and Ohmann, 2004). In addition, most understorey communities in the study area have a high potential for resilience to disturbance, owing to their rich seed banks and high resprouting capacity (Reyes and Casal, 2008; Fernández et al., 2013). Second, these forest stands grow under fairly favourable climatic conditions that result in high forest productivity (Moreno-Fernández et al., 2018) and that also can promote development of the understorey (Légaré et al., 2001). These climatic conditions may likewise help to counteract the strong light limitation imposed by these dense stands (basically managed with low thinning without understorey clearing), stimulating partial compensation (Holmgren et al., 1997) and thus allowing relatively high levels of live biomass to remain in the understorey. Third and most importantly, the complex trade-off between plant shade tolerance

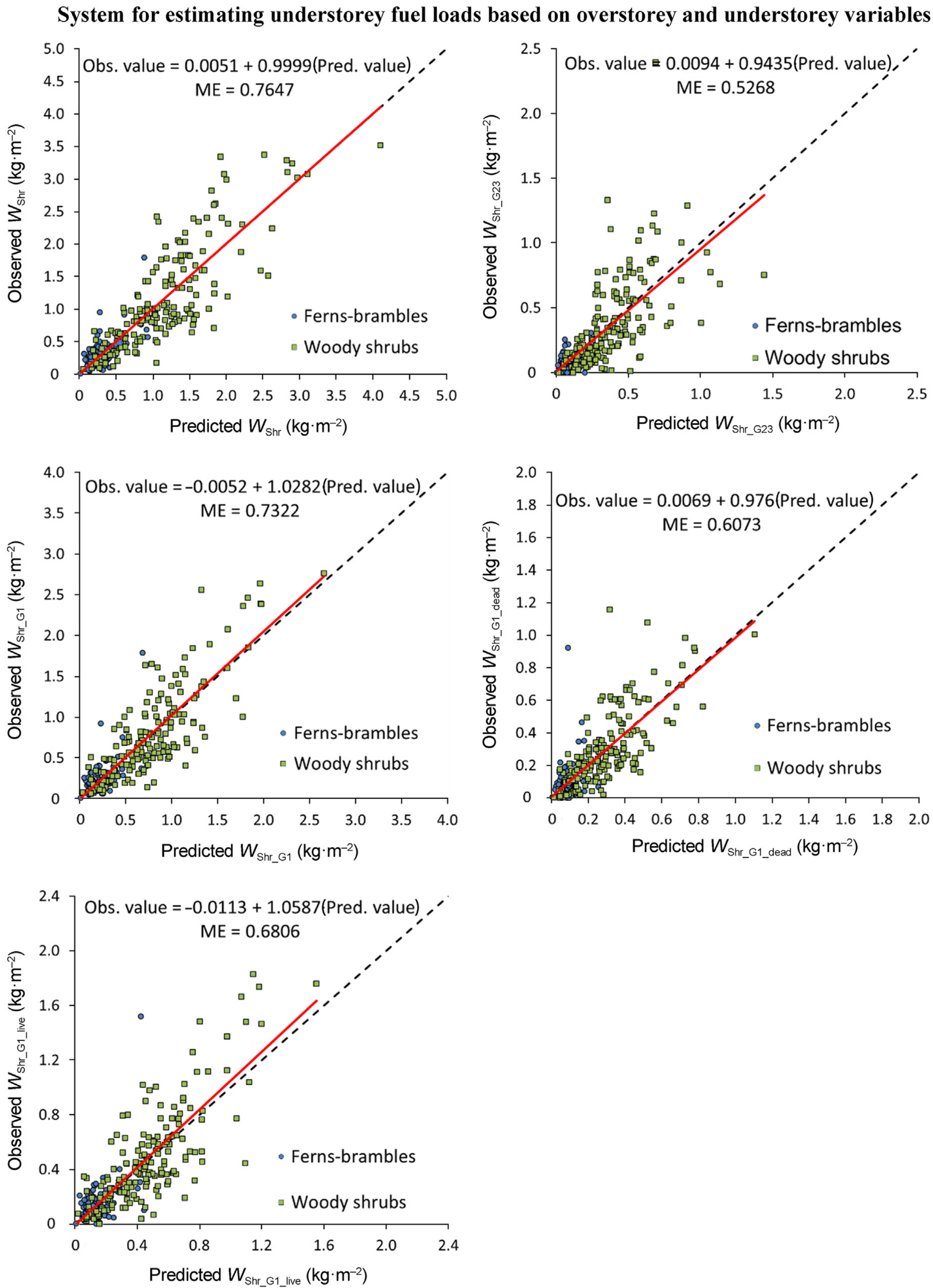

Fig. 2. Observed versus predicted values for each of the understorey fuel fractions differentiating between plots in which fern-bramble is the dominant understorey community and the other shrub-dominated communities. The red line represents the straight line fitted to the data and the dotted line represents the diagonal. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

System for estimating forest floor fuel loads based on overstorey and forest floor variables

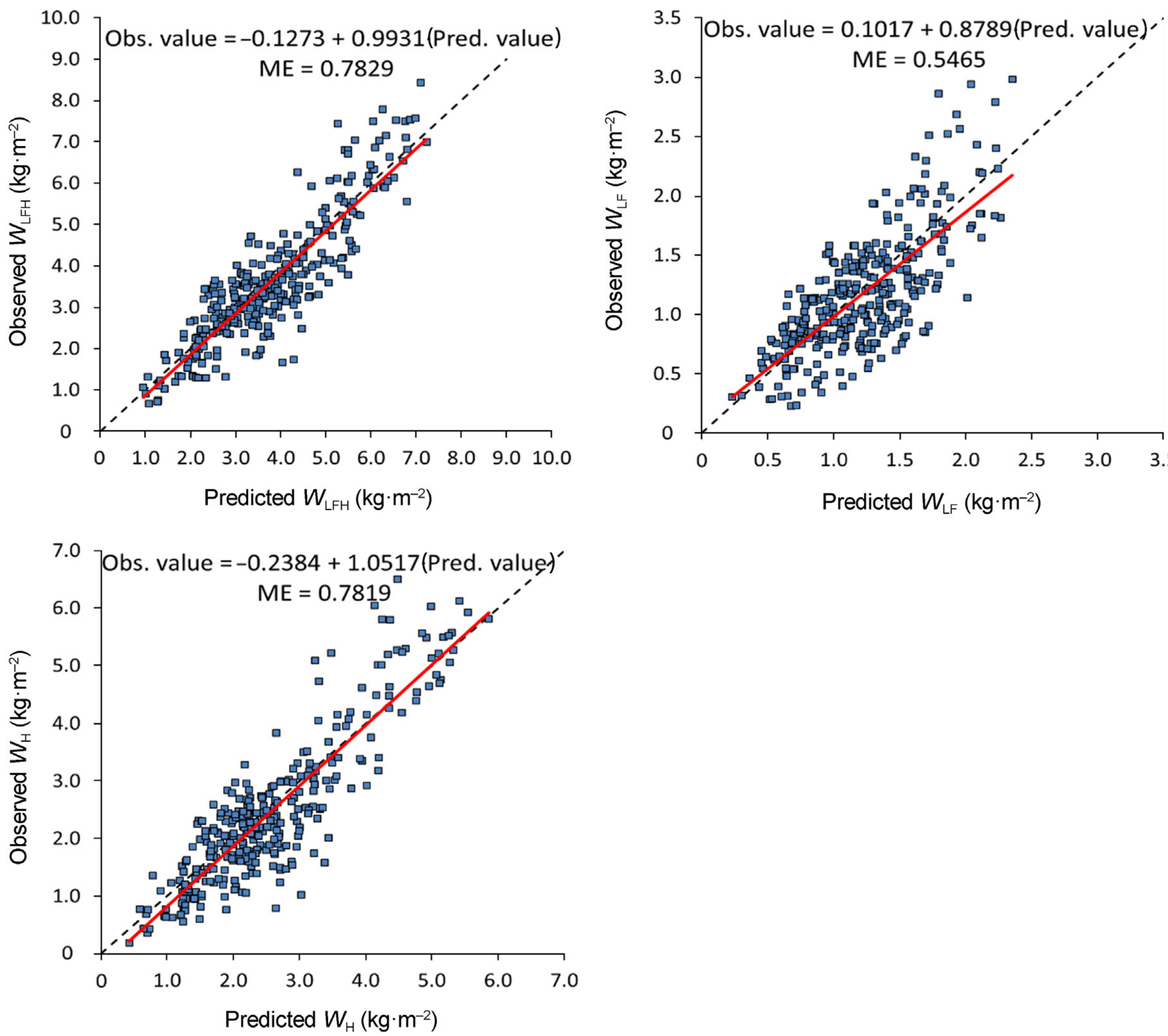

Fig. 3. Observed versus predicted values for each of the forest floor fuel fractions. The red line represents the straight line fitted to the data and the dotted line represents the diagonal. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4
Mathematical expressions of fitted models and values of goodness-of-fit statistics when only overstorey variables were considered potential independent variables.

Eq.	Mathematical expression	ME	RMSE ($kg\cdot m^{-2}$)
Equations for estimating understorey fuel loads based only on overstorey variables			
1	$\widehat{W_{Shr}} = a_0 G^{0.4021} CC_{Bliss}^{-1.2844} SDI^{-0.3886}$ with $a_0 = 2.4433 - 1.8075 I_{Pa} + 0.7029(I_{Ps} + I_{Pr})$	0.5367	0.5203
3	$\widehat{W_{Shr\_G1}} = (1.7818 - 1.0929 I_{Pa}) G^{0.4007} CC_{Bliss}^{-1.7240} SDI^{-0.3942}$	0.5213	0.3690
Equations for estimating forest floor fuel loads based only on overstorey variables			
Eq.	**Mathematical expression**	**ME**	**RMSE ($kg\cdot m^{-2}$)**
6	$\widehat{W_{LFH}} = (0.3916 + 0.2045 I_{Ps}) G^{0.5878}$	0.5157	1.0503

and drought tolerance, modulated by the plasticity to light and other plant functional traits, can play a critical role in maintaining understorey plant functionality and may have been actively operating (Holmgren et al., 2012; Delerue et al., 2013). Together with changes in the competition and facilitation process with age, and pressure due to gradients of abiotic factors (Holmgren et al., 1997; Halpern and Lutz, 2013), this defines a complex scenario regulating overstorey-understorey interactions. It is ultimately the interplay between these factors (Landuyt et al., 2019a; López-Marcos et al., 2019; Jin et al., 2022) that likely may best help to understand how shade-intolerant shrub species can persist and maintain considerable biomass under a wide range of environmental conditions like in other ecosystems (Kerns and Ohmann, 2004; Halpern and Lutz, 2013).

As expected, the observed W_{Shr} values are much lower than those observed in shrublands mainly dominated by the same species as those of understorey in the study area (Vega et al., 2022). For woody vegetation in the pine forest understorey, the average total fuel load (W_{Shr}) observed was 1.136 $kg\cdot m^{-2}$ (s.d. 0.802 $kg\cdot m^{-2}$), with a maximum value of 3.520 $kg\cdot m^{-2}$, whereas in similar shrublands, values of 2.719 $kg\cdot m^{-2}$ (s.d. 1.479 $kg\cdot m^{-2}$) and 7.316 $kg\cdot m^{-2}$ were obtained using the same sampling approach (Vega et al., 2022). The same result was obtained when comparing the average W_{Shr} of the pine understorey dominated by the fern-bramble community (0.322 $kg\cdot m^{-2}$, with a maximum value of 1.791 $kg\cdot m^{-2}$ and a standard deviation of 0.222 $kg\cdot m^{-2}$) versus treeless fern-dominated areas (1.053 $kg\cdot m^{-2}$, with a maximum value of 1.994 $kg\cdot m^{-2}$ and a standard deviation of 0.516 $kg\cdot m^{-2}$). Although these samples are not strictly comparable, because environmental and land-use history factors may be very different, they can provide initial information

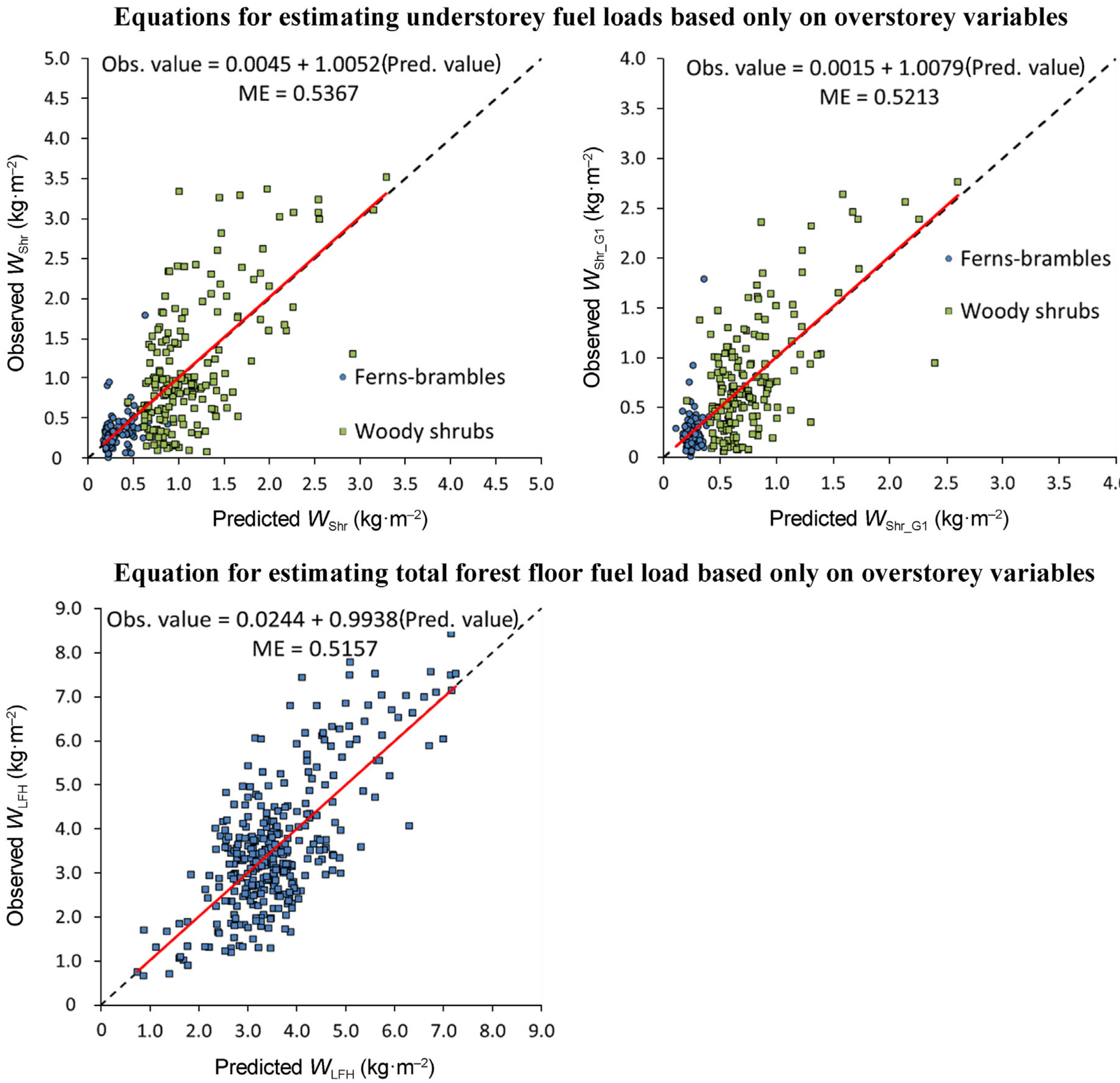

Fig. 4. Observed versus predicted values for each of the three equations fitted using only overstorey variables as regressors. For understorey fuel load equations (upper row), differentiation between sample plots in which the fern-bramble community is the dominant understorey community and the rest of the shrub-dominated communities is included. The red line represents the straight line fitted to the data and the dotted line represents the diagonal line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 5
Mathematical expressions of fitted models and values of goodness-of-fit statistics when only the transformed canopy cover fraction (CC_{Bliss}) was considered as independent variable.

Equations for estimating understorey fuel loads based only on CC_{Bliss}			
Eq.	**Mathematical expression**	**ME**	**RMSE ($kg \cdot m^{-2}$)**
1	$\widehat{W_{Shr}} = [0.6004 + 0.2752(I_{Ps} + I_{Pr})]CC_{Bliss}^{-1.5284}$	0.2626	0.6552
3	$\widehat{W_{Shr\_G1}} = [0.4106 + 0.1609(I_{Ps} + I_{Pr})]CC_{Bliss}^{-1.7357}$	0.3209	0.4533

on the main differences in fuel load.

Overall, the use of the equations fitted for shrublands in the study area (Vega et al., 2022) to estimate W_{Shr} of similar understorey formations in pine forest resulted in a mean overestimation of 0.70 $kg \cdot m^{-2}$ (84.20% of the observed average value), with an RMSE value of 0.99 $kg \cdot m^{-2}$ (119.34% of the observed average W_{Shr}). However, the use of the models fitted for shrublands to estimate the W_{LFH} tended to underestimate with a bias of 1.17 $kg \cdot m^{-2}$ (32.57% of the observed average value) and an RMSE value of 1.59 $kg \cdot m^{-2}$, which represents underestimation of 44.29% relative to the average W_{LFH} observed. In addition, the shrub bulk densities ($W_{Shr}/\overline{h_{Shr}}$) are also very different, with values of 0.56 and 1.65 $kg \cdot m^{-3}$ for understorey in fern-bramble dominated and shrub-dominated communities, and values of 1.13 and 3.62 $kg \cdot m^{-3}$, respectively, in similar shrublands. These findings confirm the importance of fitting specific fuel load estimation models for these pine stand fuel layers and advocate against extending shrubland-based results to forest understorey.

Considering the mean values of overstorey biomass of the pine species analyzed in the study area (Castedo-Dorado et al., 2012), the W_{Shr} load represented between 6% and 9% of the total aboveground biomass. The values were similar to the 6.8% reported by Gonzalez et al. (2013) for *P. pinaster* plantations in the southwest of France with understorey dominated by species also present in the Galician forests. The values observed in our study were somewhat higher than 4.7%, the mean value reported for the USA (Smith et al., 2013), while for boreal forest, values in the range 1%–13% have been reported (e.g., Merilä et al., 2014). When considering only sample plots of fern-bramble dominated understorey, shrub loads accounted for 2%–3% of the total aboveground biomass of these pine forests, which is closer to (although still higher than) the less than 1% reported by Gilliam (2007) for herbaceous understorey in the northern hemisphere.

4.1. Equations based on overstorey, understorey and forest floor variables

The observed variability explained by the system of equations for estimating shrub fuel loads from understorey and overstorey variables ranged from 53% for W_{Shr_G23} to 76% for W_{Shr}. These values are within the ranges found in other studies of understorey fuel load quantification at stand level (e.g., Kuusipalo, 1983; Porté et al., 2009; Russell et al., 2014; Nolan et al., 2022). The results are also similar to those reported by Vega et al. (2022) for treeless shrubland formations dominated by the same species as those analyzed in this study, with the exception of the coarse fuel load equation (W_{Shr_G23}) for which the estimates are somewhat less accurate in the present study. As fine fuels play an important role in the active flame phase of the fire (Rothermel, 1972; Burrows and McCaw, 1990; Fernandes et al., 2002; Fraser et al., 2016), the accuracy of the estimates obtained with the equations proposed for this fraction and its disaggregation for physiological state (live and dead) is remarkable. So far, very few studies (Hough and Albini, 1978; Fernandes and Rego, 1998; Nolan et al., 2022) have modelled understorey fine fuel load at stand-level, and we are not aware of any modelling studies of load of fine live and dead fuel fractions for the understorey vegetation.

The system of understorey fuel load equations depends on three independent variables, two characterizing the understorey layer ($\overline{h_{Shr}}$ and Cov_{Shr_Bliss}), and one characterizing the overstorey (SDI). The first two have been widely used in models for understorey load estimation, as separate variables or as phytovolume, defined as the combined variable $\overline{h_{Shr}} \times Cov_{Shr\_Bliss}$ (e.g., Fernandes et al., 2002; Heinrichs et al., 2010; Pearce et al., 2010; Gonzalez et al., 2013). The stand density index (SDI) is a widely used measure of relative density in silvicultural practice for defining management density schedules and has also been included in models for estimating shrub biomass (e.g., Moore and Deiter, 1992; Sabo et al., 2009) and for assessing the effect of canopy on understorey development (e.g., Nakajima and Tatsuhara, 2012; Fonseca and Duarte, 2017). This variable regulates the disaggregation of the fine fuel load by physiological status (live and dead), i.e., it drives the dead ratio ($W_{Shr\_G1\_dead}/W_{Shr\_G1}$), probably due to the importance of the influence of this variable on light interception and, therefore, on understorey structural characteristics (Lochhead and Comeau, 2012; Parker, 2014).

As expected, the parameters associated with the presence of fern-bramble dominated understories in the W_{Shr}, W_{Shr_G1} and W_{Shr_G23} models (Eqs. 1–3) were negative and significant, which implies that the fuel load estimates for these formations are lower than those for the shrub communities, assuming the same values for the independent variables of each model.

Regarding the dominance of different pine species in the overstorey, the parameters associated with the dominance of *P. sylvestris* and *P. radiata* in the total understorey fuel load model (Eq. 1) were positive and significant. This implies that, if the independent variables are considered equal, the total shrub fuel load estimates for these species are higher than those estimated for *P. pinaster* stands. That result was not expected due to the known high light transmittance in *P. pinaster* (Gonzalez et al., 2013), which is greater than that of *P. sylvestris* in the region (Silva-Pando et al., 2002). However, factors such as provenance, age and sylvicultural management, which affect crown structure and LAI, influence the effects of light transmittance (e.g., Sonohat et al., 2004). The differences in understorey biomass that depend on the overstorey composition may be partly due to differences in average understorey bulk density. The distribution of the observed values of bulk density for the three species is shown in Fig. 5. The *t*-test for comparison of means

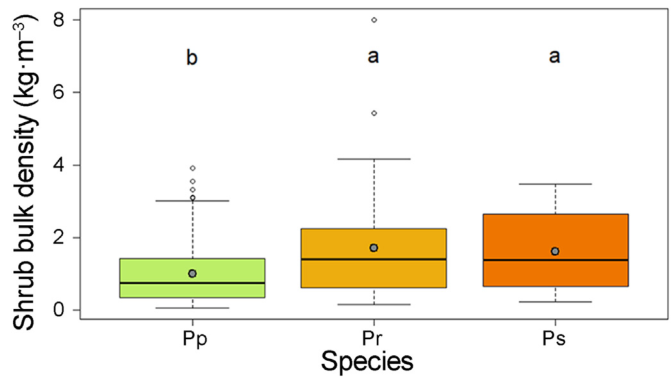

Fig. 5. Box-plot of observed shrub bulk density (kg·m^{-3}) by pine species (Pp = *Pinus pinaster*; Pr = *Pinus radiata* and Ps = *Pinus sylvestris*). Different letters indicate significant differences between mean values (α = 0.05). Grey dots represent mean values.

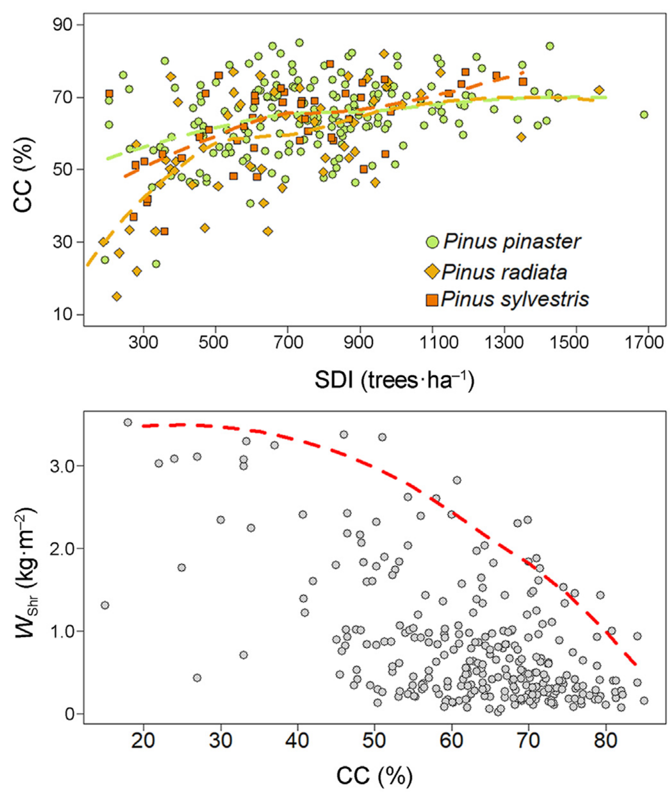

Fig. 6. (Upper figure) Scatter plot of observed SDI (trees·ha^{-1}) versus observed CC (%) by pine species. The dashed lines represent the loess regression (span = 0.9) fitted to CC values for each species. (Lower figure) Scatter plot of observed CC (%) versus observed W_{Shr}. The red dashed line represents the loess regression (span = 0.9) fitted to the 95th percentile values of W_{Shr}. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

indicated a significantly lower value for *P. pinaster* with no significant differences between the other two species. On the other hand, there were also differences in the relationship between the SDI value and the CC percentage (Fig. 6a), so that for CC values below 65%, the same SDI value corresponds to lower CC percentages in *P. sylvestris* and specially in *P. radiata* than in *P. pinaster* and, therefore, lower light interception, favouring development of the understorey. For CC values higher than 65%, the curves show the same behaviour for both *P. radiata* and *P. pinaster*, with slightly higher values for *P. sylvestris*; however, the effect on understorey growth was not very pronounced, as values above a threshold of 60%–70% cover showed a large reduction in understorey biomass (Fig. 6b). Similar results were reported by Ahmad et al. (2019) for larch plantations in China, suggesting an optimal value of 70% CC to reach high levels of overstorey biomass and adequate levels of understorey biomass maintaining numerous other forest ecosystem services.

The dominance of *P. sylvestris* in the overstorey also showed a significant effect on the equations for disaggregation of the total fuel load (W_{Shr}) on coarse (W_{Shr_G23}, Eq. 2) and fine fuel loads (W_{Shr_G1}, Eq. 3). Thus, considering the remaining independent variables to be equal, the coarse load is increased in *P. sylvestris*-dominated stands. The main reason is the difference in the shrub fine fuel ratio (W_{Shr_G1}/W_{Shr}) observed in the sample plots of the three species (Fig. 7), with a significantly lower value in the case of *P. sylvestris* according to the mean comparison analysis ($\alpha = 0.05$). This response seems to be related to the greater presence of *Erica australis* L.-dominated understorey in *P. sylvestris*, as the observed fine fuel ratio of this community was significantly lower (0.620; s.d. 0.15) than in the *Ulex* sp.-dominated communities (0.732; s.d. 0.16), the latter more frequent in *P. pinaster* and *P. radiata* stands.

Regarding the forest floor layers equations, the independent variables included in the models were the depth of the total of the three layers ($\overline{d_{LFH}}$), the ratio between the depth of the LH layers and the total depth of the three layers ($\overline{d_{LF}}/\overline{d_{LFH}}$), and the stand basal area (G). The depth of these layers has shown to be a good predictor variable in pine stands (e.g., Fernandes et al., 2002; Stephens et al., 2004; Arellano-Pérez, 2011; DiMario et al., 2018). Stand basal area has also been included as a predictor variable in forest floor load estimation models owing to its effect on the amount of annual needle litterfall in pine ecosystems (e.g., Berg et al., 1999; Fernandes et al., 2002; Starr et al., 2005) and its spatial distribution (e.g., Penne et al., 2010; Lado-Monserrat et al., 2016; López-Senespleda et al., 2021) finally affecting the forest floor fuel load. Our models also show the significant effect of *P. sylvestris* dominance in the overstorey on the total forest floor layer (W_{LFH}) relative to the other two pine species, with a mean value of the total fuel load of 49.81 Mg·ha^{-1} (s.d. 2.00 Mg·ha^{-1}) versus 32.54 Mg·ha^{-1} (s.d. 0.99 Mg·ha^{-1}) for *P. pinaster* and 34.07 Mg·ha^{-1} (s.d. 1.56 Mg·ha^{-1}) for *P. radiata*. Similar results were reported by López-Senespleda et al. (2021) for pine species in peninsular Spain, although with somewhat lower values for *P. pinaster*. This probably reflects the higher productivity of maritime pine stands in NW Spain and seems consistent with the influence of annual precipitation and latitude on W_{LFH}, detected by those authors, both larger in Galicia stands than most of Iberian Peninsula. In our case the differences due to overstorey species were expected given that the fuel load in the litter layer is strongly affected by the amount of aboveground biomass and the litter decomposition rates. The amount of aboveground biomass include understorey and overstorey biomass; the first is significantly higher in *P. sylvestris* and *P. radiata* stands than in *P. pinaster* stands (see Table 1); regarding the overstorey biomass, according to Fernández-Alonso et al. (2013), in the study area the canopy fuel load (CFL, defined as the fuel load of needles and fine twigs) is significantly higher in *P. sylvestris* stands (CFL mean value of 10.4 Mg·ha^{-1}) than in *P. radiata* (CFL mean value of 7.2 Mg·ha^{-1}) and *P. pinaster* stands (CFL mean value of 6.1 Mg·ha^{-1}). Litter layer decomposition rates are driven by the nature of the microbial community and other parameters, mainly litter quality and climatic conditions (Berg et al., 1999; Zhang et al., 2008). The *P. sylvestris* stands in the study area are located at significantly higher mean altitude (1,026 m a.s.l.; s.d. 265 m a.s.l.) than those of the other two pine species (*P. pinaster* 478 m a.s.l.; s.d. 294 m a.s.l.) and *P. radiata* (475 m a.s.l.; s.d. 190 m a.s.l.), and with significantly lower average annual temperature (9.7 °C; s.d. 1.1 °C) for *P. sylvestris* than for *P. pinaster* (12.3 °C; s.d. 1.4 °C) and *P. radiata* (11.9 °C; s.d. 1.2 °C). This is likely to result in lower litter decomposition rates (Dawud et al., 2017) and therefore a greater litter depth ($\overline{d_{LFH}}$), especially on the H layer ($\overline{d_{H}}$) in this species (see Table 2).

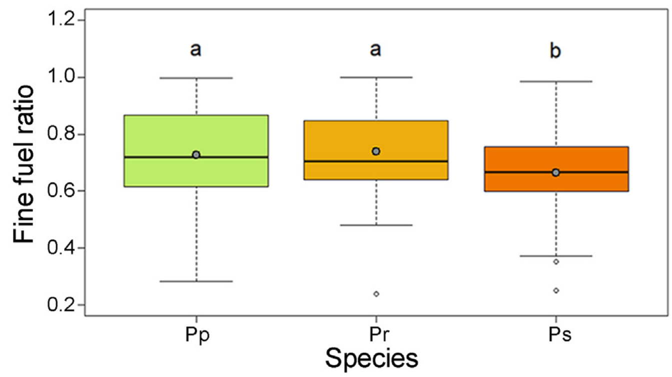

Fig. 7. Box-plot of observed shrub fine fuel ratio by pine species (Pp = *Pinus pinaster*; Pr = *Pinus radiata* and Ps = *Pinus sylvestris*). Different letters indicate significant differences between mean values ($\alpha = 0.05$). Grey dots represent mean values.

4.2. Equations only based on overstorey variables

Prediction of understorey community biomass based only on overstorey variables is inherently difficult, as these communities are heterogeneous aggregates, in various seral states and strongly influenced by their location and historical disturbances, both natural and anthropogenic (Suchar and Crookston, 2010; Botequim et al., 2015; Johnson et al., 2017; Landuyt et al., 2019b). The latter is especially important in pine stands in NW Spain, in which establishment, composition and structure are strongly affected by human action, and with a high level of variability of understorey communities for the same dominant pine species (Botequim et al., 2015). This difficulty is reflected in the fact that it was not possible to fit equation systems for the understorey and the forest floor loads, and only separate equations were fitted for the total (W_{Shr}) and fine shrub fuels (W_{Shr_G1}) and for the total forest floor load (W_{LFH}). The three equations explain slightly more than 50% of the observed variability and the independent variables included in the models were SDI, CC and G for the understorey fuel load models and G for the total forest floor fuel load model (W_{LFH}). These three variables are strongly related to competition for resources such as light, nutrients, space and soil water between understorey and overstorey and, therefore, an increase in the overstorey competition will usually leads to a reduction in the understorey biomass (e.g., González-Hernández et al., 1998; Sabo et al., 2009; Ares et al., 2010; Pimont et al., 2018).

Basal area (G) has been shown to be a limiting factor in understorey shrub biomass (e.g., Coll et al., 2011; Castedo-Dorado et al., 2012; Russell et al., 2014; Botequim et al., 2015; Mitsopoulos and Xanthopoulos, 2016), although sometimes weak (Halpern and Lutz, 2013) or even no relationships are detected (Porté et al., 2009; Gonzalez et al., 2013); however, its effect on the W_{Shr} and W_{Shr_G1} estimating equations is apparently contradictory (positive exponent). This is due to the combined effect of the three independent variables (G, SDI and CC), with a fuel load reduction effect by increasing the canopy cover and the relative spacing index, so that when these two variables (CC and SDI) are equal, a greater basal area probably implies a higher site quality and therefore more resources available for growth of vegetation (Krebs et al., 2019).

Regarding the total forest floor fuel load equation, G was the only independent variable that had a positive effect on estimates, i.e., an increase in G values implies an increase in fuel load, mainly due to a higher biomass in the overstorey, the main fuel sources for the litter layer, in line with previous findings (Hough and Albini, 1978; Fernandes et al., 2002; Parresol et al., 2012; Lydersen et al., 2015). The dominance of ferns-brambles in the understorey community and the dominance of different pine species in the overstorey also affected the estimates of these equations in the same way as previously discussed for the systems of equations dependent on understorey and overstorey variables.

Finally, the two models fitted for total and fine understorey vegetation fuel loads based only on canopy cover (CC_{Bliss}) explained 26% and 32% of the observed variability, respectively (Table 5). These models therefore have a low predictive capacity, like other models obtained in similar studies (Russell et al., 2014; Botequim et al., 2015). These models suggest that light availability, closely linked to overstorey cover, may be the most limiting factor for the understorey biomass in the dense stands of the study area. This seems to be consistent with the prevailing mild climate conditions in NW Spain, particularly in terms of thermal regime and water availability, which favour high site productivity. In any case, the main advantage of those models is that in forested landscapes, understorey vegetation is largely invisible to remote sensing, in contrast to some structural features of the canopy, which can be estimated with moderate accuracy. At present, the development of broad spatial scales mapping of understorey fuel loads depends on inferences about their relationships with remotely observable features (McKenzie et al., 2009) and the proposed models for W_{Shr} and W_{Shr_G1} based only on canopy cover fulfil this requirement. Therefore, maps of the spatial distribution of these understory variables could be generated by estimating canopy cover from information derived from the Spanish national coverage of small-footprint ALS data (0.5–2.0 first return·m^{-2}).

5. Conclusions

Fuel reduction operations should be a key element in the management of forest stands, especially in the case of the pine forests analyzed here, which are prone to suffering intense wildfires. As wildfire protection resources are not unlimited, it is essential to optimize decision making to focus fuel management on strategic locations to minimize fire hazard at landscape scale. For this purpose, it is central to have tools that allow detailed, accurate characterization of forest fuel complexes. This requirement will be even more critical in the future, as predicted climate change scenarios include drier conditions with a consequent increase in fire hazard.

In this study, two additive systems of equations that allow estimation of the fuel load of the understorey vegetation and forest floor layers were developed for the three main pine species in NW of Spain from variables that are easy to measure in the field. The novel systems distinguish between understories dominated by woody shrub and fern-bramble communities, providing accurate estimates differentiated by fuel size and, in the case of fine fuels, by physiological state (dead or alive), contributing to filling a large knowledge gap. These models, together with those previously developed for canopy fuels for the same species in the same geographical area, will enable accurate structural characterization of understorey and overstorey fuels in the region and from a practical point of view will be very useful for evaluating fire behaviour and defining fuel management prescriptions. These equations may also be of great benefit in other areas given the ecological importance of the understorey and the effect of its biomass on, for example, biodiversity, competitive interaction with tree species regeneration or energy flows and water and nutrient cycles. Moreover, the independent variables included in the proposed equations are commonly measured in the Spanish National Forest Inventory to evaluate different ecosystem services, so that, without additional costs, they would allow estimating additional information of great utility for forest managers.

The proposed equation systems based on combining overstorey variables with understorey or forest floor variables present robust and accurate estimates, despite the inherent problem of modelling in a highly variable landscape with strong stochasticity of site conditions, a long history of land use and disturbances. This variability may explain the modest results for estimating fuel fractions based only on overstorey variables, emphasizing that forest overstorey-understorey and overstorey-soil organic layers relationships are very complex and that other variables not available in this study may improve predictions. Nevertheless, the present results are encouraging because they illustrate the feasibility of the stand-level approach to developing operational models of understorey and forest floor layer fuel loads.

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Authors' contributions

José A. Vega: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Supervision, Project administration, Funding acquisition. **Stéfano Arellano-Pérez**: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft. **Juan Gabriel Álvarez-González**: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft. **Cristina Fernández**: Data curation, Writing – original draft. **Enrique Jiménez**: Data curation, Writing – original draft. **Pedro Cuiñas**: Data curation, Writing – original draft. **José María Fernández-Alonso**: Data curation, Writing – original draft. **Daniel J. Vega-Nieva**: Data curation, Writing – original draft. **Fernando Castedo-Dorado**: Data curation, Writing – original draft. **Cecilia Alonso-Rego**: Data curation, Writing – original draft. **Teresa Fontúrbel**: Data curation, Supervision, Writing – original draft, Project administration, Funding acquisition. **Ana Daría Ruiz-González**: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

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

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References

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211 (1–2), 83–96.
Ahmad, B., Wang, Y., Hao, J., Liu, Y., Bohnett, E., Zhang, K., 2019. Optimizing stand structure for tradeoffs between overstory and understory vegetation biomass in a larch plantation of Liupan Mountains, Northwest China. For. Ecol. Manage. 443, 43–50.
Alexander, M.E., Cruz, M.G., 2011. Crown fire dynamics in conifer forests. In: Werth, P.A., Potter, B.E., Clements, C.B., Finney, M.A., Goodrick, S.C., Alexander, M.E., Cruz, M.G., Forthofer, J.A., McAllister, S.S. (Eds.), Synthesis of Knowledge of Extreme Fire Behavior, Volume I for Fire Managers. Gen. Tech. Rep. PNW-GTR-854, Portland, pp. 107–142.

Arellano, S., Vega, J.A., Ruiz-González, A.D., Arellano, A., Álvarez-González, J.G., Vega, D.J., Pérez, E., 2017. Foto-guía de combustibles forestales de Galicia y comportamiento del fuego asociado. Andavira, Santiago de Compostela, Spain.
Arellano-Pérez, S., 2011. Modelos de combustibles forestales de Galicia. MSc Thesis. Universidad de Santiago de Compostela, Lugo, Spain, p. 388.
Ares, A., Neill, A.R., Puettmann, K.J., 2010. Understory abundance, species diversity and functional attribute response to thinning in coniferous stands. For. Ecol. Manage. 260 (7), 1104–1113.
Augusto, L., Dupouey, J.L., Ranger, J., 2003. Effects of tree species on understory vegetation and environmental conditions in temperate forests. Ann. For. Sci. 60 (8), 823–831.
Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. For. Ecol. Manage. 254 (1), 1–15.
Berg, B., Albrektson, A., Berg, M.P., Cortina, J., Johansson, M.B., Gallardo, A., Madeira, M., Pausas, J., Kratz, W., Vallejo, R., McClaugherty, C., 1999. Amounts of litter fall in some pine forests in a European transect, in particular Scots pine. Ann. For. Sci. 56 (8), 625–639.
Bliss, C., 1938. The transformation of percentages for use in the analysis of variance. Ohio J. Sci. 38, 9–12.
Boch, S., Berlinger, M., Fischer, M., Knop, E., Nentwig, W., Türke, M., Prati, D., 2013. Fern and bryophyte endozoochory by slugs. Oecologia 172 (3), 817–822.
Boeken, B., Orenstein, D., 2001. The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. J. Veg. Sci. 12, 825–832.
Botequim, B., Zubizarreta-Gerendiain, A., Garcia-Gonzalo, J., Silva, A., Marques, S., Fernandes, P.M., Pereira, J.M.C., Tomé, M., 2015. A model of shrub biomass accumulation as a tool to support management of Portuguese forests. iForest 8, 114–125.
Brown, J.K., Oberhau, R.D., Johnston, C.M., 1982. Handbook for inventorying surface fuels and biomass in the interior west. USDA For. Serv. Gen. Tech. Rep. INT-GTR-129 48.
Burgan, R.E., Rothermel, R.C., 1984. BEHAVE: fire behaviour prediction and fuel modeling system - FUEL subsystem. USDA For. Serv. Gen. Tech. Rep. INT- 167, 126.
Burrows, N.D., McCaw, W.L., 1990. Fuel characteristics and bushfire control in banksia low woodlands in Western Australia. J. Environ. Manag. 31, 229–236.
Burton, J.E., Cawson, J.G., Filkov, A.I., Penman, T.D., 2021. Leaf traits predict global patterns in the structure and flammability of forest litter beds. J. Ecol. 109 (3), 1344–1355.
Byram, G.M., 1959. Combustion of forest fuels. In: Davis, K.P. (Ed.), Forest Fire: Control and Use. McGraw-Hill, New York, USA.
Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. J. For. 39, 388–394.
Casado, M.A., Castro, I., Ramírez-Sanz, L., Costa-Tenorio, M., de Miguel, J.M., Pineda, F.D., 2004. Herbaceous plant richness and vegetation cover in Mediterranean grasslands and shrublands. Plant Ecol. 170 (1), 83–91.
Castedo-Dorado, F., Gómez-Vázquez, I., Fernandes, P.M., Crecente-Campo, F., 2012. Shrub fuel characteristics estimated from overstory variables in NW Spain pine stands. For. Ecol. Manage. 275, 130–141.
Coll, L., González-Olabarria, J.R., Mola-Yudego, B., Pukkala, T., Messier, C., 2011. Predicting understory maximum shrubs cover using altitude and overstory basal area in different Mediterranean forests. Eur. J. For. Res. 130, 55–65.
Cruz, M.G., de Mar, P.J., Adshead, D., 2011. Radiata Pine Plantation Fuel and Fire Behaviour Guide. CSIRO and GHD publication for the Australian Government Department of Agriculture, Fisheries and Forestry, Camberra, ACT, p. 23.
Dale, V.H., Beyeler, S.C., Jackson, B., 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA. Ecol. Indicat. 1 (3), 155–170.
Dawud, S.M., Vesterdal, L., Raulund-Rasmussen, K., 2017. Mixed-species effects on soil C and N stocks, C/N ratio and pH using a transboundary approach in adjacent common garden Douglas-fir and beech stands. Forests 8, 95.
Delerue, F., Gonzalez, M., Atlan, A., Pellerin, S., Augusto, L., 2013. Plasticity of reproductive allocation of a woody species (*Ulex europaeus*) in response to variation in resource availability. Ann. For. Sci. 70 (3), 219–228.
DiMario, A.A., Kane, J.M., Jules, E.S., 2018. Characterizing forest floor fuels surrounding large sugar pine (*Pinus lambertiana*) in the Klamath Mountains, California. Northwest Sci. 92 (3), 181–190.
Eckstein, R.L., Donath, T.W., 2005. Interaction between litter and water availability affect seedling emergence in four familial pairs of floodplain species. J. Ecol. 93, 807–816.
Federer, C.A., 1982. Subjectivity in the separation of organic horizons of the forest floor. Soil Sci. Soc. Am. J. 46, 1090–1093.
Fernandes, P.M., Rego, F.C., 1998. Equations for estimating fuel load in shrub communities dominated by *Chamaespartium tridentatum* and *Erica umbellata*. In: Proceedings of the 3rd International Conference on Forest Fire Research and 14th Fire and Forest Meteorology Conference, pp. 16–20.
Fernandes, P.M., Rigolot, E., 2007. The fire ecology and management of maritime pine (*Pinus pinaster* Ait.). For. Ecol. Manage. 241, 1–13.
Fernandes, P., Loureiro, C., Botelho, H., Ferreira, A., Fernandes, M., 2002. Avaliaçao indirecta de carga de combustivel em Pinhal Bravo. Silv. Lusit. 10 (1), 73–90.
Fernandes, P.A.M., Loureiro, C., Botelho, H.S., 2004. Fire behaviour and severity in a maritime pine stand under differing fuel conditions. Ann. For. Sci. 61, 537–544.
Fernandes, P.M., Botelho, H.S., Rego, F.C., Loureiro, C., 2009. Empirical modelling of surface fire behaviour in maritime pine stands. Int. J. Wildland Fire 18, 698–710.
Fernández, C., Vega, J.A., Fonturbel, T., 2013. Does fire severity influence shrub resprouting after spring prescribed burning? Acta Oecol. 48, 30–36.
Fernández-Alonso, J.M., Alberdi, I., Álvarez-González, J.G., Vega, J.A., Cañellas, I., Ruiz-González, A.D., 2013. Canopy fuel characteristics in relation to crown fire potential in pine stands: analysis, modelling and classification. Eur. J. For. Res. 132, 363–377.
Finney, M.A., 1998. FARSITE: Fire Area Simulator–Model Development and Evaluation. Research Paper RMRS-RP-4 Revised. USDA For. Serv., Rocky Mountain Research Station, Ogden, UT, p. 47.
Fonseca, T.F., Duarte, J.C., 2017. A silvicultural stand density model to control understory in maritime pine stands. iForest 10, 829–836.
Fraser, I.P., Williams, R.J., Murphy, B.P., Camac, J.S., Vesk, P.A., 2016. Fuels and landscape flammability in an Australian–alpine environment. Austral Ecol. 41, 657–670.
Geddes, N., Dunkerley, D.L., 1999. The influence of organic litter on the erosive effects of raindrops and of gravity drops released from desert shrubs. Catena 36 (4), 303–313.
George, L.O., Bazzaz, F.A., 2014. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. In: Gillam, F.S. (Ed.), The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, NY, pp. 340–355.
Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57 (10), 845–858.
Giuggiola, A., Zweifel, R., Feichtinger, L.M., Vollenweider, P., Bugmann, H., Haeni, M., Rigling, A., 2018. Competition for water in a xericforest ecosystem – effects of understory removal on soil micro-climate, growth and physiology of dominant Scots pine trees. For. Ecol. Manage. 409, 241–249.
Gonzalez, M., Augusto, L., Gallet-Budynek, A., Xue, J., Yauschew-Raguenes, N., Guyon, D., Trichet, P., Delerue, F., Niollet, S., Andreasson, F., Achat, D.L., Bakker, M.R., 2013. Contribution of understory species to total ecosystem aboveground and belowground biomass in temperate *Pinus pinaster* Ait. Forests. For. Ecol. Manage. 289, 38–47.
González-Hernández, M.P., Silva-Pando, F.J., Casal Jiménez, M., 1998. Production patterns of understory layers in several Galician (NW Spain) woodlands. Seasonality, net productivity and renewal rates. For. Ecol. Manage. 109, 251–259.
Halpern, C.B., Lutz, J.A., 2013. Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecol. Monogr. 83 (2), 221–237.
Harvey, A.C., 1976. Estimating regression models with multiplicative heteroscedasticity. Econometrica 44, 461–465.
Heinrichs, S., Bernhardt-Roemermann, M., Schmidt, W., 2010. The estimation of aboveground biomass and nutrient pools of understorey plants in closed Norway spruce forests and on clearcuts. Eur. J. For. Res. 129, 613–624.
Helluy, M., Gavinet, J., Prévosto, B., Fernandez, C., 2021. Influence of light, water stress and shrub cover on sapling survival and height growth: the case of *A. unedo, F. ornus* and *S. domestica* under Mediterranean climate. Eur. J. For. Res. 140 (3), 635–647.
Helms, J.A., 1998. The Dictionary of Forestry. Society of American Foresters, p. 210.
Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. Ecology 78 (7), 1966–1975.
Holmgren, M., Gómez-Aparicio, L., Quero, J.L., Valladares, F., 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia 169 (2), 293–305.
Hough, W.A., Albini, F.A., 1978. Predicting Fire Behavior in Palmetto-Gallberry Fuel Complexes. Research Paper SE-RP-174. USDA-Forest Service, Southeastern Forest Experiment Station, Asheville, NC, pp. 1–48.
Jin, Y., Liu, C., Qian, S.S., Luo, Y., Zhou, R., Tang, J., Bao, W., 2022. Large-scale patterns of understory biomass and its allocation across China's forests. Sci. Total Environ. 804, 150169.
Johnson, K., Domke, G., Russell, M., Walters, B., Hom, J., Peduzzi, A., Birdsey, R., Dolan, K., Huang, W., 2017. Estimating aboveground live understory vegetation carbon in the United States. Environ. Res. Lett. 12, 125010.
Kerns, B.K., Ohmann, J.L., 2004. Evaluation and prediction of shrub cover in coastal Oregon forests (USA). Ecol. Indicat. 4 (2), 83–98.
Krebs, M.A., Reeves, M.C., Baggett, L.S., 2019. Predicting understory vegetation structure in selected western forests of the United States using FIA inventory data. For. Ecol. Manage. 448, 509–527.
Kuusipalo, J., 1983. Mustikan varvuston biomassamäärän vaihtelusta erilaisissa metsiköissä. Silv. Fenn. 17 (3), 245–257 (in Finnish).
Lado-Monserrat, L., Lidon, A., Bautista, I., 2016. Litterfall, litter decomposition and associated nutrient fluxes in *Pinus halepensis*: influence of tree removal intensity in a Mediterranean forest. Eur. J. For. Res. 135, 203–214.
Landuyt, D., De Lombaerde, E., Perring, M.P., Hertzog, L.R., Ampoorter, E., Maes, S.L., De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B.K., Wang, B., Wasof, S., Verheyen, K., 2019a. The functional role of temperate forest understorey vegetation in a changing world. Global Change Biol. 2511, 3625–3641.
Landuyt, D., Maes, S.L., Depauw, L., Ampoorter, E., Blondeel, H., Perring, M.P., Brūmelis, G., Brunet, J., Decocq, G., Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kirby, K.J., Kopecký, M., Máliš, F., Wulf, M., Verheyen, K., 2019b. Drivers of above-ground understorey biomass and nutrient stocks in temperate deciduous forests. J. Ecol. 108 (3), 982–997.
Légaré, S., Bergeron, Y., Leduc, A., Paré, D., 2001. Comparison of the understory vegetation in boreal forest types of southwest Quebec. Can. J. Bot. 79 (9), 1019–1027.
Levia Jr., D.F., Frost, E.E., 2003. A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. J. Hydrol. 274 (1–4), 1–29.
Lochhead, K.D., Comeau, P.G., 2012. Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. For. Ecol. Manage. 284, 12–22.

López-Marcos, D., Turrión, M.B., Bravo, F., Martínez-Ruiz, C., 2019. Understory response to overstory and soil gradients in mixed versus monospecific Mediterranean pine forests. Eur. J. For. Res. 138 (6), 939–955.
López-Senespleda, E., Calama, R., Ruiz-Peinado, R., 2021. Estimating forest floor carbon stocks in woodland formations in Spain. Sci. Total Environ. 788, 147734.
Lydersen, J.M., Collins, B.M., Knapp, E.E., Roller, G.B., Stephens, S., 2015. Relating fuel loads to overstorey structure and composition in a fire-excluded Sierra Nevada mixed conifer forest. Int. J. Wildland Fire 24 (4), 484–494.
Madrigal, J., Marino, E., Guijarro, M., Hernando, C., Díez, C., 2012. Evaluation of the flammability of gorse (*Ulex europaeus* L.) managed by prescribed burning. Ann. For. Sci. 69 (3), 387–397.
MARM, 2011. Cuarto Inventario Forestal Nacional. Comunidad Autónoma de Galicia. Dirección General del Medio Natural y Política Forestal, Madrid, España.
Martínez-Cortizas, A., Pérez-Alberti, A., 1999. Atlas climático de Galicia. Xunta de Galicia, Santiago de Compostela. Spain.
McKenzie, D., Crystal, L.R., Cushman, S.A., 2009. Modeling understory vegetation and its response to fire. In: Millspaugh, J.J., Thompson III, F.R. (Eds.), Models for Planning Wildlife Conservation in Large Landscapes. Elsevier, Burlington, USA, pp. 391–414.
Merilä, P., Mustajärvi, K., Helmisaari, H.S., Hilli, S., Lindroos, A.J., Nieminen, T.M., Nöjd, P., Rautio, P., Salemaa, M., Ukonmaanaho, L., 2014. Above-and below-ground N stocks in coniferous boreal forests in Finland: implications for sustainability of more intensive biomass utilization. For. Ecol. Manage. 311, 17–28.
Mitsopoulos, I., Xanthopoulos, G., 2016. Effect of stand, topographic, and climatic factors on the fuel complex characteristics of Aleppo (*Pinus halepensis* Mill.) and Calabrian (*Pinus brutia* Ten.) pine forests of Greece. For. Ecol. Manage. 360, 110–121.
Moore, M.M., Deiter, D.A., 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. J. Range Manag. 45, 267–271.
Moore, P.T., Van Miegroet, H., Nicholas, N.S., 2007. Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce–fir forest. Can. J. For. Res. 37 (12), 2689–2700.
Moreno-Fernández, D., Álvarez-González, J.G., Rodríguez-Soalleiro, R., Pasalodos-Tato, M., Cañellas, I., Montes, F., Díaz-Varela, E., Sánchez-González, M., Crecente-Campo, F., Álvarez-Álvarez, P., Barrio-Anta, M., Pérez-Cruzado, C., 2018. National-scale assessment of forest site productivity in Spain. For. Ecol. Manage. 417, 197–207.
Myers, R.H., 1990. Classical and Modern Regression with Applications, second ed. Duxbury Press, Belmont, California.
Nakajima, T., Tatsuhara, S., 2012. Silviculture guidelines for developing mixed forests in old coniferous plantations under long-rotation stand density control. For. Sci. Tech. 8 (3), 127–134.
Nolan, R.H., Price, O.F., Samson, S.A., Jenkins, M.E., Rahmani, S., Boer, M.M., 2022. Framework for assessing live fine fuel loads and biomass consumption during fire. For. Ecol. Manage. 504, 119830.
Parker, W.C., 2014. The relationship of stand structure with canopy transmittance: simple models and practical methods for managing understory light conditions in eastern white pine (*Pinus strobus* L.)-dominated forests. For. Chron. 90 (4), 489–497.
Parresol, B.R., Blake, J.I., Thompson, A.J., 2012. Effects of overstory composition and prescribed fire on fuel loading across a heterogeneous managed landscape in the southeastern USA. For. Ecol. Manage. 273, 29–42.
Pearce, H.G., Anderson, W.R., Fogarty, L.G., Todoroki, C.L., Anderson, S.A.J., 2010. Linear mixed-effects models for estimating biomass and fuel loads in shrublands. Can. J. For. Res. 40, 2015–2026.
Penne, C., Ahrends, B., Deurer, M., Böttcher, J., 2010. The impact of the canopy structure on the spatial variability in forest floor carbon stocks. Geoderma 158, 282–297.
Perala, D.A., Alban, D., 1993. Allometric Biomass Estimators for Aspen-Dominated Ecosystems in the Upper Great Lakes. USDA, Forest Service, North Central Forest Experiment Station. Research Paper NC-314.
Pimont, F., Dupuy, J.L., Rigolot, E., 2018. A simple model for shrub-strata-fuel dynamics in *Quercus coccifera* L. communities. Ann. For. Sci. 75 (2), 1–9.
Porté, A.J., Samalens, J.-C., Dulhoste, R., Teissier Du Cros, R., Bosc, A., Meredieu, C., 2009. Using cover measurements to estimate aboveground understorey biomass in Maritime pine stands. Ann. For. Sci. 66, 307.
Powell, T.L., Gholz, H.L., Clark, K.L., Starr, G., Cropper Jr., W.P., Martin, T.A., 2008. Carbon exchange of a mature, naturally regenerated pine forest in north Florida. Global Change Biol. 14, 2523–2538.
Pyne, S.J., Andrews, P.L., Laven, R.D., 1996. Introduction to Wildland Fire, second ed. John Wiley & Sons, New York, USA.
Qiao, Y., Miao, S., Silva, L.C., Horwath, W.R., 2014. Understory species regulate litter decomposition and accumulation of C and N in forest soils: a long-term dual-isotope experiment. For. Ecol. Manage. 329, 318–327.
Reyes, O., Casal, M., 2008. Regeneration models and plant regenerative types related to the intensity of fire in Atlantic shrubland and woodland species. J. Veg. Sci. 19 (4), 575–583.
Rothermel, R.C., 1972. A Mathematical Model for Predicting Fire Spread in Widland Fuels. Res. Pap. INT-115, Ogden, UT, p. 40.
Rue-Johns, A.Z., Crotteau, J.S., D'Amore, D.V., Barnard, J.C., 2021. Biomass regressions for understory species in young-growth Sitka spruce–western hemlock forests of southeast Alaska. Northwest Sci. 95 (1), 114–124.
Russell, M.B., D'Amato, A.W., Schulz, B.K., Woodall, C.W., Domke, G.M., Bradford, J.B., 2014. Quantifying understorey vegetation in the US Lake States: a proposed framework to inform regional forest carbon stocks. Forestry 87, 629–638.
Russell, M.B., Woodall, C.W., Potter, K.M., Walters, B.F., Domke, G.M., Oswalt, C.M., 2017. Interactions between white-tailed deer density and the composition of forest understories in the northern United States. For. Ecol. Manage. 384, 26–33.
Russell-Smith, J., Murphy, B.P., Meyer, C.P., Cook, G.D., Maier, S., Edwards, A.C., Schatz, J., Brocklehurst, P., 2009. Improving estimates of savanna burning emissions for greenhouse accounting in northern Australia: limitations, challenges, applications. Int. J. Wildland Fire 18, 1–18.
Sabo, K.E., Sieg, C.H., Hart, S.C., Bailey, J.D., 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. For. Ecol. Manage. 257, 1656–1662.
SAS Institute Inc, 2004. SAS/ETS© 9.1 User's Guide. SAS Institute Inc, Cary, NC.
Scott, J.H., Burgan, R.E., 2005. Standard Fire Behavior Fuel Models: a Comprehensive Set for Use with Rothermel's Surface Fire Spread Model. USDA For. Serv., Rocky Mountain Research Station, General Technical Report RMRS-GTR-153, p. 72.
Scott, J.H., Reinhardt, E.D., 2001. Assessing Crown Fire Potential by Linking Models of Surface and Crown Fire Behavior. Res. Pap. RMRS-RP-29. USDA, Forest Service, Rocky Mountain Research Station, p. 59.
Sigurdsson, B.D., Magnusson, B., Elmarsdottir, A., Bjarnadottir, B., 2005. Biomass and composition of understory vegetation and the forest floor carbon stock across Siberian larch and mountain birch chronosequences in Iceland. Ann. For. Sci. 62 (8), 881–888.
Silva-Pando, F.J., González-Hernández, M.P., Rozados-Lorenzo, M.J., 2002. Pasture production in a silvopastoral system in relation with microclimate variables in the Atlantic coast of Spain. Agrofor. Syst. 56 (3), 203–211.
Smith, J.E., Heath, L.S., Hoover, C.M., 2013. Carbon factors and models for forest carbon estimates for the 2005–2011 National Greenhouse Gas Inventories of the United States. For. Ecol. Manage. 307, 7–19.
Sonohat, G., Balandier, P., Ruchaud, F., 2004. Predicting solar radiation transmittance in the understory of even-aged coniferous stands in temperate forests. Ann. For. Sci. 61 (7), 629–641.
Starr, M., Saarsalmi, A., Hokkanen, T., Merilä, P., Helmisaari, H.-S., 2005. Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. For. Ecol. Manage. 205, 215–225.
Stephens, S.L., Finney, M.A., Schantz, H., 2004. Bulk density and fuel loads of ponderosa pine and white fir forest floors: impacts of leaf morphology. Northwest Sci. 78 (2), 93–110.
Suchar, V.A., Crookston, N.L., 2010. Understory cover and biomass indices predictions for forest ecosystems of the Northwestern United States. Ecol. Indicat. 10, 602–609.
Tkacz, B., Riitters, K., Percy, K.E., 2013. Forest monitoring methods in the United States and Canada: an overview. Dev. Environ. Sci. 12, 49–73.
Vega, J.A., 2001. Efectos del fuego prescrito sobre el suelo en pinares de *Pinus pinaster* Ait. de Galicia. PhD Thesis. Universidad Politécnica de Madrid.
Vega, J.A., Fernández, C., Fonturbel, T., 2005. Throughfall, runoff and soil erosion after prescribed burning in gorse shrubland in Galicia (NW Spain). Land Degrad. Dev. 16, 37–51.
Vega, J.A., Fontúrbel, T., Merino, A., Fernández, C., Ferreiro, A., Jiménez, E., 2013. Testing the ability of visual indicators of soil burn severity to reflect changes in soil chemical and microbial properties in pine forests and shrubland. Plant Soil 369, 73–91.
Vega, J.A., Arellano-Pérez, S., Álvarez-González, J.G., Fernández, C., Jiménez, E., Fernández- Alonso, J.M., Vega-Nieva, D.J., Briones-Herrera, C., Alonso-Rego, C., Fontúrbel, T., Ruiz-González, A.D., 2022. Modelling aboveground biomass and fuel load components at stand level in shrub communities in NW Spain. For. Ecol. Manage. 505, 119926.
Xunta de Galicia, 2022. Plan de prevención y defensa contra los incendios forestales de Galicia (PLADIGA). Consellería do Medio Rural. Dirección Xeral de defensa do monte 259. https://mediorural.xunta.gal/sites/default/files/temas/forestal/pladiga/2022/01_Memoria_Pladiga_2022_Gal.pdf. (Accessed 15 October 2022).
Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93.