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RESEARCH PAPER

Scaling-up individual-level allometric equations to predict stand-level fuel loading in Mediterranean shrublands

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Abstract

• ***Key message*** **Allometric biomass equations developed for individual shrubs can be applied to estimate shrubland fuels from measurements of cover and average height by species.**

• ***Context*** Shrubs are a major component of surface fuels in many fire-prone ecosystems. Shrub fuel loading is often estimated by "double sampling", where data from a destructive vegetation survey is used to model vegetation-fuel relationships (development phase), and these relationships are then applied to vegetation data from a second survey (application phase). Vegetation-fuel relationships can be modeled at different levels of vegetation detail, from individual plants to stands, but the increased effort of detailed measurements may compromise large-scale applications.

• ***Aims*** To facilitate fuel loading assessments in Mediterranean shrublands, we present and test a novel method to estimate stand-level shrub loading that consists in applying individual-level allometric equations to vegetation plot data collected by measuring the percent cover and mean height of each shrub species.

• ***Methods*** We used individual-level data (i.e., plant dimensions and dry weights) to develop allometric equations for total and fine (leaves and branches < 6 mm) biomass of 26 Mediterranean shrub species. We then evaluated the accuracy and precision of the proposed method in comparison to an approach assuming constant bulk density, using data from 131 vegetation plots and taking as benchmark stand-level loading estimates derived by aggregation of individual biomass allometric estimates. A second set of 13 plots was used to quantify the additional error derived from visual estimation of species mean height and cover.

• ***Results*** The performance of species-specific models was acceptable in estimating total and fine biomass at the individual level. When based on species mean height and cover data, stand-level fuel loading estimates calculated using the proposed method had a better precision and accuracy than those obtained using bulk density values (− 4 vs. + 39% in relative bias; 10 vs. 40% in relative MAE). Visual estimation of species mean height and percent cover led to 10 and 16% increase in MAE for species loading estimates of total and fine fuels, respectively, with respect to estimates obtained without this source of error.

• ***Conclusions*** Our approach to estimate shrub loading allows combining fast species-level vegetation sampling with the flexibility of individual-level allometries to model to size-related variations of bulk density.

Keywords Bulk density · Fine fuels · Fuel loading · Fuel mapping · Vegetation sampling

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Contribution of co-authors PC, XC, and EG coordinated field sampling. MCA and PC conducted the analyses and led manuscript writing, with contributions from all co-authors.

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1 Introduction

Shrubs are a major component of surface fuels in many fire-prone ecosystems such as shrublands, encroached grasslands, woodlands, and forests, especially under low tree density (Sabo et al. 2009; Coll et al. 2011). Key shrub fuel descriptors such as loading, bulk density, dead-to-live ratio, and moisture are required inputs to wildfire behavior models (Keane 2015). Due to their high rate of energy exchange, shrub fine fuels (i.e., leaves and fine branches < 6 mm diameter) are particularly important to fire ignition and spread (Pyne 1984). Properties of shrub fine fuels are related not only to short-term meteorological conditions but also to long-term responses to natural (e.g., drought, browsing, tree canopy cover) and anthropogenic (e.g., management) factors (Castro et al. 2003; Pimont et al. 2018; Ruffault et al. 2018). Moreover, shrub fuel properties exhibit a strong interspecific variation. For example, *Pistacia lentiscus* L. always has a low percentage of twigs in relation to total biomass, and *Genista scorpius* (L.) DC. in Lam. et DC. has a high proportion of standing dead material (Papió and Trabaud 1991). Fuel properties have been linked to functional species groups related to post-fire regeneration strategies (Saura-Mas et al. 2010; Vilagrosa et al. 2014). The diversity of morphological, physiological, and phenological traits of woody plant species coexisting in the shrub complex results in high spatial and temporal heterogeneity of fuel properties.

Fuel load (i.e., dry weight of fuel per surface area) is arguably the most important property when studying wildland fuels, and it can be estimated using a panoply of approaches (Keane 2015). Although destructive methods, such as clipping and weighting, are generally the most accurate to estimate fuel load of shrub complexes, they are also expensive and time consuming (Catchpole and Wheeler 1992; Bonham 2013). Since destructive sampling is inefficient when the goal is to make an inventory of shrub fuels over large spatial extents or to monitor their dynamics over time (Keane 2015), the so called "double sampling" approaches are often adopted. The first sampling phase involves collecting a number of destructive samples to model the relationship between fuel load and previously measured vegetation dimensions. This relationship can then be applied in a second sampling phase where vegetation dimensions are either measured in field campaigns or obtained through remote sensing (Kerr and Ostrovsky 2003). Different kinds of relationships have been developed for different levels of detail in vegetation sampling (Catchpole and Wheeler 1992), from individual plant measurements to stand-level measurements of vegetation cover and height (Fig. 1).

At the individual level, allometric equations are commonly used to estimate plant biomass from individual plant measurements (usually crown dimensions, plant height, or basal stem diameter; see arrow "1-1" in Fig. 1). Allometric relationships for shrub species have been developed in different regions to estimate both total biomass (Armand et al. 1993; Usó et al. 1997; Blanco-Oyonarte and Navarro-Cerrillo 2003; Conti et al. 2013) and fine fuel fractions (Pereira et al. 1995; Paton et al. 2002; Huff et al. 2017). Despite being flexible enough to accommodate variations in bulk density related to plant size, allometric equations have some limitations. They may not have the same predictive ability in all sites where the species occurs, as a result of either different environmental conditions (e.g., forest canopy cover; browsing; fire) or genetic factors affecting plant morphology (Catchpole and Wheeler 1992; López-Serrano et al. 2005; Ritchie et al. 2013; Pimont et al. 2018). Moreover, it often happens that species-specific equations are lacking for some of the species found in the target area. This can be solved using allometries developed for morphologically or functionally similar species groups (Conti et al. 2013; Casals et al. 2016). However, the potential decrease in the predictive ability incurred by using allometries derived from group-specific instead of species-specific relationships needs to be quantified (Sah et al. 2004).

Identifying and tallying all individual woody plants in fixed area plots becomes expensive for large-scale fuel surveys, which leads to the development of vegetation-fuel relationships at coarser levels. Habitat-specific empirical relations to predict shrub fuel loading can be fitted from stand-level measurements such as visual estimates of total cover, mean height, or apparent volume of the shrub layer (Pasalodos-Tato et al. 2015) (see arrow "3-3" in Fig. 1). These relationships are faster to apply than approaches requiring individual plant measurements and are interesting because of the possibility to obtain estimates over large areas with remote sensing technologies (Kerr and Ostrovsky 2003). Nevertheless, empirical relationships developed from stand-level data may have low predictive ability due to spatial variability in species composition (even within the same habitat) and between-species differences in size-biomass relationships.

Between the individual and stand levels of vegetation sampling detail lies the species level, which consists in estimating dimensions of each species in the study plot, such as species mean height and cover. Species-level data have the advantage of allowing between-species morphological variability to be accounted for. Developing approaches to estimate fuel loading from species data is appealing because mean height and percent cover of understory species are routinely recorded in national forest inventory surveys (e.g., Villanueva 2004). To obtain loading estimates from species data, one can calculate the apparent volume occupied by each species and multiply it by species-specific bulk density values (Fernandes 2009) or use an allometric relationship similar to stand-level approaches (Porté et al. 2009; Ruiz-Peinado et al. 2013) (see arrow "2-2" in Fig.1).

With the aim to facilitate regional assessments of fuel loading (or forage availability, or carbon stock) in Mediterranean shrublands, the main goal of this study is to present and

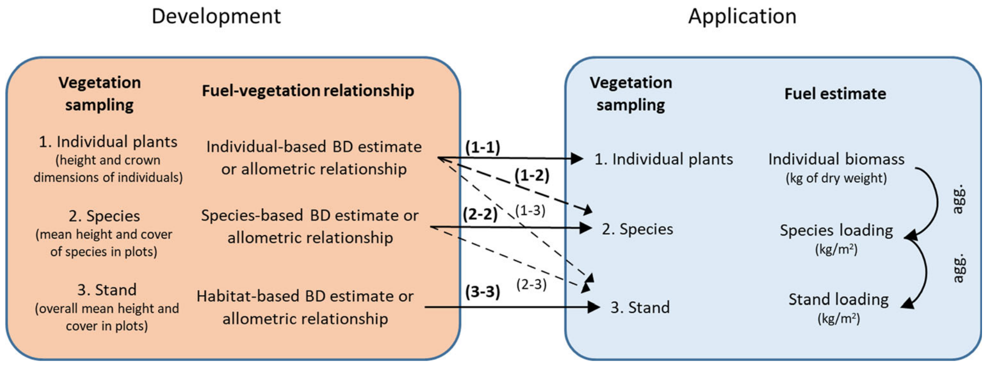

Fig. 1 Conceptual diagram to illustrate different ways to estimate fuel loading by "double sampling" (i.e., first sampling phase to obtain data to model fuel-vegetation relationships and second sampling phase where such relationships are applied). Continuous arrows ("1-1," "2-2," and "3-3") indicate "double sampling" approaches in which the two phases are conducted with the same detail of vegetation sampling. The approach evaluated in this paper is indicated using a thick dashed arrow ("1-2"), implying a development phase at the individual level and an application at the species level. Other approaches (i.e., thin dashed arrows "1-3" and "2-3") are mentioned in the "Discussion" section. BD stands for "bulk density." Fuel loading estimates at species/stand levels may be obtained by aggregation (agg.) of estimates obtained at lower levels

evaluate a method to estimate shrub loading that consists in developing allometric equations at the individual level and applying them to vegetation plot data sampled by measuring percent cover and mean height of each species (see arrow "1-2" in Fig. 1). We start with the development of individual-level allometric equations for total fuel biomass, fine fuel biomass, and crown projected area of 26 shrub species of the target region (Catalonia; NE of Spain). For those species sampled in more than one site, we compare the performance of species-specific vs. site-specific equations. We also assess the loss of predictive capacity when allometries are calibrated for functional groups. After that, we detail the proposed method to estimate fuel loading and we use data from 131 vegetation plots to evaluate its predictive capacity in comparison to an approach assuming constant species bulk density. Finally, we use a second set of 13 plots to quantify the additional error derived from visual estimation of species mean height and percent cover.

2 Material and methods

2.1 Study area

The study area is Catalonia (NE of Iberian Peninsula; Fig. 2). The region is highly mountainous with the exception of the southwestern plains of the Ebro basin. Elevation ranges from sea level up to 3000 m, with a mean elevation of about 700 m. Soil parent materials are most commonly limestones and marls, though low metamorphic schists and granodiorites are also frequent in the north and north-east and evaporites in the central-western area. Mediterranean is the dominant climate, but climatic variation is high following variation in topography and continentality.

2.2 Target species and vegetation sampling

Our dataset for calibration of fuel allometries is a collection of destructive individual-level field data obtained by different research groups (Table 4 Appendix 1). The selection of species aims to include the most common shrubs in Catalonia. Specimens were sampled in a single location, but in nine species specimens include two or three sampling locations to account for geographic variation of morphology (Table 4 Appendix 1). The dataset includes 26 species belonging to three plant forms: Macro-phanerophytes, nano-phanerophytes, and chamaephytes (Table 5 Appendix 1). Nano-phanerophytes are, in turn, split on the basis of their post-fire regeneration strategy (i.e., obligate seeders, facultative seeders, and resprouters), according to Paula et al. (2009).

2.3 Development of allometric equations

Power functions are often used to study the relationship between individual volume and its corresponding total or fine fuel biomass (Armand et al. 1993; Pereira et al. 1995; Paton et al. 2002; Ruiz-Peinado et al. 2013). The following functions were used to model total dry weight (B_{total}; in kg) and fine fuel dry weight (B_{fine}; in kg) of individuals:

$$B_{total} = a_{total} \cdot V^{b_{total}} \quad (1.1)$$

$$B_{fine} = a_{fine} \cdot V^{b_{fine}} \quad (1.2)$$

where V is the apparent shrub volume (in m^3) assuming the shape of an elliptic cylinder, and a_{total}, a_{fine}, b_{total}, and b_{fine} are species-specific (or group-specific) parameters. Parameter a represents the bulk density for a shrub of 1 m^3, so its value depends on how volume is defined (Pereira et al. 1995). We did not consider alternative forms of solid bodies for the calculation of apparent volume (Blanco-Oyonarte and Navarro-

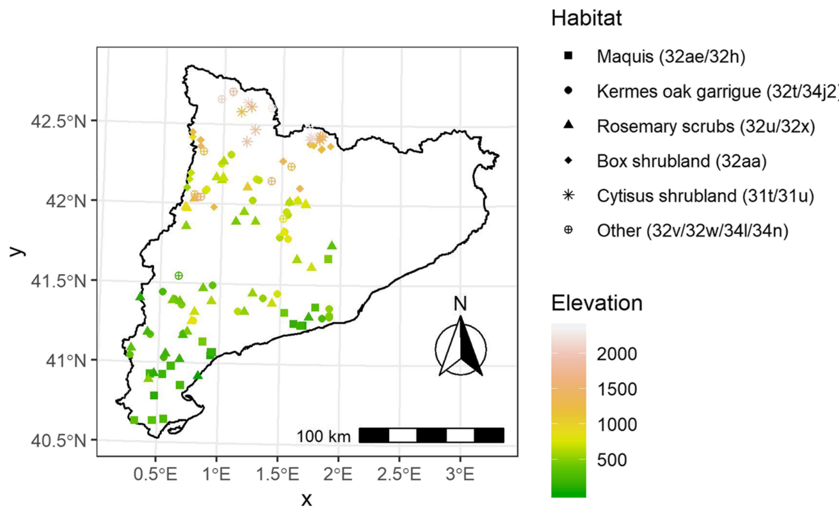

Fig. 2 Map of the location of the 131 10 × 10-m plots distributed across the western and central parts of Catalonia (NE Spain) and used for the evaluation of the proposed loading estimation method. Colors indicate the elevation at the plot site (gray indicates a missing elevation value) and shapes correspond to habitat classes

Cerrillo 2003), because this often leads to proportional *a* values (Usó et al. 1997). Parameter *b* represents the degree of isometry/allometry in the relationship between volume and biomass. It can be understood as the ratio between relative biomass increments and relative volume increments, with values below one indicating that bulk density decreases with plant volume (Armand et al. 1993).

Coefficients for volume-biomass allometries were obtained by fitting generalized linear models (GLMs) with a logarithm link function and assuming Gamma-distributed errors (McCullagh and Nelder 1989):

$$log(E(B)) = log(a) + b \cdot log(V) \quad \text{with} \quad B \sim Gamma(\mu, \nu) \tag{2}$$

where $\mu = E(B)$ and ν are the mean and dispersion parameters of the Gamma distribution, respectively. GLMs directly fit the expected mean of the dependent variable, hence avoiding the biases of log-log linear regressions (McCullagh and Nelder 1989). The predictive value of allometric equations was assessed by calculating the cross-validated (leave-one-out) bias, mean absolute error (MAE), and coefficient of determination (R^2) between the predicted and observed individual biomass. For the nine species where different locations had been sampled, we evaluated the degree of generality of species-specific allometries by comparing them to models including the location factor as potentially affecting both the intercept and the slope of the relationship:

$$log(E(B)) = log(a_l) \cdot L + b_l \cdot log(V) \cdot L \quad \text{with} \quad B \sim Gamma(\mu, \nu) \tag{3}$$

where L is an indicator variable of location, and a_l and b_l are location-specific parameters. Models fitted by either Eq. (2) or (3) were compared in terms of predictive value and by means of a likelihood ratio chi-square test. We also evaluated to which extent allometric equations calibrated after grouping the species into functional groups had similar or worse predictive capacity than species-specific allometries. For that, we fitted group-specific allometric equations (Eqs. (1) and (2)), again using GLMs with logarithm link and Gamma distribution of errors. As before, we compared the models of Eqs. (2) and (3), but replacing the role of location by that of species identity.

2.4 Application of the individual-level allometries to species-level data

When vegetation data consist in mean height (H_m; in cm) and the percent cover (C; in %) per shrub species, we suggest to calculate species fuel loading (kg m^{-2}) by applying the allometries developed at the individual level to an "average" individual and multiply the resulting biomass by an estimation of plant density. This requires developing an additional allometry to estimate the projected crown area (CA; cm^2) of individuals from their height H (cm):

$$\text{CA} = a_{area} \cdot H^{b_{area}} \tag{4}$$

where, as before, a_{area} and b_{area} are species-specific (or group-specific) parameters. Applying Eq. (4) on H_m provides CA_m, the area occupied by an average individual. Multiplying H_m by CA_m (after expressing them in m and m^2, respectively), one obtains the apparent volume of the average individual (V_m; in m^3). Biomass allometries (Eq. (1)) can then be applied to obtain $B_{total,m}$ or $B_{fine,m}$ estimates corresponding to the average individual. Note that the whole process is equivalent to a single allometric equation relating biomass to height, which in the case of $B_{total,m}$ is

$$B_{total,m} = a_{total} \cdot (H_m \cdot CA_m)^{b_{total}} = a_{total} \cdot (a_{area})^{b_{total}} \cdot (H_m)^{(1+b_{area}) \cdot b_{total}}. \tag{5}$$

Finally, the loading of the species in the target area (W; in kg m^{-2}) is estimated as the product of $B_{total,m}$ or $B_{fine,m}$ and N, an estimate of density of individuals (in m^{-2}) derived from percent cover:

$$N = (C \cdot 100)/CA_m \quad (6)$$

$$W_{total} = N \cdot B_{total,m} \quad (7.1)$$

$$W_{fine} = N \cdot B_{fine,m} \quad (7.2)$$

We estimated parameters a_{area} and b_{area} of Eq. (4) by fitting GLMs with Gamma errors (Eqs. (2) and (3)). We fitted Eq. (4) and not Eq. (5) because explicit CA_m estimates are needed for Eq. (6). Crown area allometries were evaluated with the same procedure used for fuel biomass.

2.5 Evaluation of the proposed method

We evaluated the performance of the method presented in the previous section using data from 131 10 × 10-m plots distributed across the eastern and central parts of Catalonia (Fig. 2) and surveyed by forest rangers ("Cos d'Agents Rurals de la Generalitat de Catalunya"). On each plot, rangers tallied all shrub individuals (height and crown dimensions) within two 90°-angle belt transects of 10 m length and 1 m width. Individual-level biomass estimates were obtained using plant measurements to calculate shrub volume (V), as explained in Appendix 1, and applying Eq. (1) with species- or group-specific allometric coefficients (Table 6 Appendix 2). Biomass estimates were then aggregated into species and stand loading values (in kg m^{-2}), which were taken as benchmarks to evaluate the predictive value of estimates derived from species-level data.

Estimates of mean height (H_m) and percent cover (C) by species were calculated from individual-level measurements: H_m was calculated as a weighted average of individual heights, using crown area as weight, whereas C was calculated as the sum of crown areas and expressed in percent of the sampled area (20 m^2). One species cover value exceeded 100% due to crown overlap and was truncated. These species-level estimates contain very little measurement error, so they are appropriate to assess the predictive capacity of loading estimation methods while controlling for sampling uncertainty (see next section). We compared the performance of two approaches to estimate species and stand fuel loading:

1. Bulk density: We multiplied C and H_m to obtain a species apparent volume per square meter, which we then multiplied by the species-specific (or group-specific) mean bulk density values (Table 5 Appendix 1).
2. Up-scaled allometries: We estimated the CA_m from H_m, using species-specific (or group-specific) crown area allometries (Eq. (4); Table 6 Appendix 2). Biomass values for "average individuals" were then estimated using (species- or group-specific) allometries (Eq. (1); Table 6 Appendix 2). Finally, species loadings were obtained using Eqs. (6) and (7).

We assessed the predictive value of the two approaches by calculating bias, mean absolute error (MAE), and coefficient of determination (R^2) of the resulting species and stand loading estimates with respect to the benchmark values.

2.6 Quantification of the error derived from visual vegetation sampling

Estimates of species C and H_m contain more or less measurement error depending on the sampling method (Catchpole and Wheeler 1992; Bonham 2013). To address the effect of this additional source of error, we selected a second set of 13 5 × 5 m vegetation plots where vegetation sampling was conducted both at the individual level (tallies) and at the species level (visually). Species visual C and H_m estimates were made by three different researchers and were averaged to decrease observer bias. We compared the predictive performance of our proposed loading estimation method from either (a) species data obtained by aggregation of individual measurements (as in the previous section) or (b) species data estimated visually. As before, benchmarks for the evaluation were species loadings obtained from aggregation of individual biomass estimates.

3 Results

3.1 Performance of individual-level allometric equations

Bulk density of sampled individuals varied broadly among species and individuals, with species mean values ranging between 0.26 kg m^{-3} (*Viburnum tinus*) and 7.94 kg m^{-3} (*Thymus vulgaris*) for total biomass and between 0.21 kg m^{-3} (*V. tinus*) and 3.22 kg m^{-3} (*Cistus laurifolius*) for fine fuel biomass (Table 5 Appendix 1). Cross-validated predictive performance of individual-level allometries was highest for total biomass (W_{total}; relative MAE = 36%; rel. bias + 6%; R^2 = 0.84), closely followed by fine fuel biomass (W_{fine}; rel. MAE = 43%; rel. bias + 4%; R^2 = 0.75), whereas the worst performance was obtained for crown area allometries (CA; rel. MAE = 56%; rel. bias + 5%; R^2 = 0.58) (Table 1). The predictive performance of allometries decreased when calibrating equations for functional groups, leading to an + 18–20% increase in MAE for biomass estimates and a + 6% increase for crown area estimates, with respect to species-specific models (Table 1). Table 6 Appendix 2 includes details of fitted allometric coefficients and cross-validated predictive performance

Table 1 Cross-validated predictive performance (mean absolute error [MAE], bias, and coefficient of determination [R^2]) of individual-level allometric equations for total biomass, fine fuel biomass, and projected crown area. The first two rows show the predictive performance of species- and group-specific allometries. The predictive performance of the nine species subset with different populations sampled is shown in the last two rows, including or not the location factor. Table 6 shows the allometric coefficients and predictive performance for every species and functional group

		Total biomass (B_{total})			Fine fuels (B_{fine})			Crown area (*CA*)		
Allometries fitted by…	*n*	MAE (kg) [%]	Bias (kg) [%]	R^2	MAE (kg) [%]	Bias (kg) [%]	R^2 (%)	MAE (cm^2) [%]	Bias (cm^2) [%]	R^2 (%)
Species	795	0.438 [36.0%]	+ 0.070 [+ 5.7%]	0.839	0.284 [42.6%]	+ 0.028 [+ 4.2%]	0.751	4291 [56.1%]	+ 372 [+ 4.9%]	0.579
Functional groups	795	0.654 [53.8%]	− 0.072 [− 5.9%]	0.633	0.425 [62.3%]	+ 0.024 [+ 3.6%]	0.446	4744 [62.1%]	+ 239 [+ 3.1%]	0.425
Species (subset)	431	0.374 [44.5%]	+ 0.025 [+ 3.0%]	0.756	0.224 [44.1%]	+0.009 [+ 1.7%]	0.695	3291 [55.2%]	+ 179 [+ 3.0%]	0.602
Species and location	431	0.357 [42.4%]	− 0.009 [− 1.1%]	0.629	0.192 [38.0%]	− 0.018 [− 3.5%]	0.649	2888 [48.5%]	+ 128 [+ 2.1%]	0.577

values for each species and functional group. We found significant differences between location-specific (Eq. (3)) and species-specific (Eq. (2)) models for total biomass in five of the nine species where different localities had been sampled (*p-LRT* in Table 6 Appendix 2). When location was included, relative MAE decreased from 45 to 42% for total biomass and from 44 to 38% for fine fuels (Table 1).

3.2 Evaluation of the proposed method

The total number of individuals tallied in the 131 vegetation plots was 6900, and the number of individuals per plot ranged between 8 and 148. Among all individuals, 72% belonged to species for which species-specific allometric models were available. The remaining were assigned the allometric parameter values of their corresponding functional group. Total loading in plots ranged from 0.03 to 2.60 kg m^{-2} (average 0.81 kg m^{-2}) and that of fine fuels from 0.03 to 1.76 kg m^{-2} (average 0.54 kg m^{-2}).

Calculation of percent cover (C) and mean height (H_m) by species resulted in 830 species records. Species and stand loadings calculated using species-level data and species mean bulk density estimates correlated quite strongly with values obtained from aggregation of individual biomass estimates (Table 2). However, medium and large loading values were often overestimated with respect to benchmark values (Fig. 3) and the overall relative bias was + 39% for total fuel and + 27% for fine fuel. Estimates derived from the proposed method based on up-scaled allometries were substantially more accurate and precise that those derived from bulk density (Table 2; see also Tables 7 and 8 Appendix 2). MAE of the proposed method was 0.017 kg m^{-2} (14%) for total fuel at the species level and 0.082 kg m^{-2} (10%) at the stand level, and slightly larger errors occurred for fine fuels. Small negative biases were however observed (− 4% relative bias for total fuel and − 5% for fine fuel; Table 2).

3.3 Vegetation sampling effect on loading estimates

The second dataset of 13 25-m^2 vegetation plots included 518 individuals and 49 species cover/height records. The proposed approach tended to overestimate species loading in this dataset (Table 3; Fig. 4), but the smaller sample size ($n = 49$) leads to performance statistics that have larger variance than in the previous dataset ($n = 830$). Visual estimation of species C and H_m produced a moderate increase + 0.022 kg m^{-2} (+ 10%) in MAE for total fuel and + 0.022 kg m^{-2} (+ 16%) for fine fuel; differences in bias were small for both fuel fractions.

Table 2 Predictive performance (mean absolute error [MAE], bias, and coefficient of determination [R^2]) of species and stand loadings calculated from species data using either species mean bulk density values ("bulk density") or the proposed method based on individual-level allometries ("up-scaled allometries"). In all cases, benchmark loadings are those obtained from aggregation of individual biomass estimates. Brackets for MAE and bias indicate relative values

		Species loading ($n = 830$)			Stand loading ($n = 131$)		
Fraction	Method	MAE (kg m^{-2}) [%]	Bias (kg m^{-2}) [%]	R^2	MAE (kg m^{-2}) [%]	Bias (kg m^{-2}) [%]	R^2
Total fuel (W_{total})	Bulk density	0.054 [42.9%]	+ 0.049 [+ 38.5%]	0.911	0.322 [39.8%]	+ 0.311 [+ 38.5%]	0.900
	Up-scaled allometries	0.017 [13.6%]	− 0.005 [− 3.7%]	0.971	0.082 [10.2%]	− 0.030 [− 3.7%]	0.951
Fine fuel (W_{fine})	Bulk density	0.037 [43.0%]	+ 0.023 [+ 27.3%]	0.803	0.175 [32.4%]	+ 0.147 [+ 27.3%]	0.831
	Up-scaled allometries	0.016 [18.7%]	− 0.004 [− 4.8%]	0.913	0.074 [13.7%]	− 0.025 [− 4.6%]	0.879

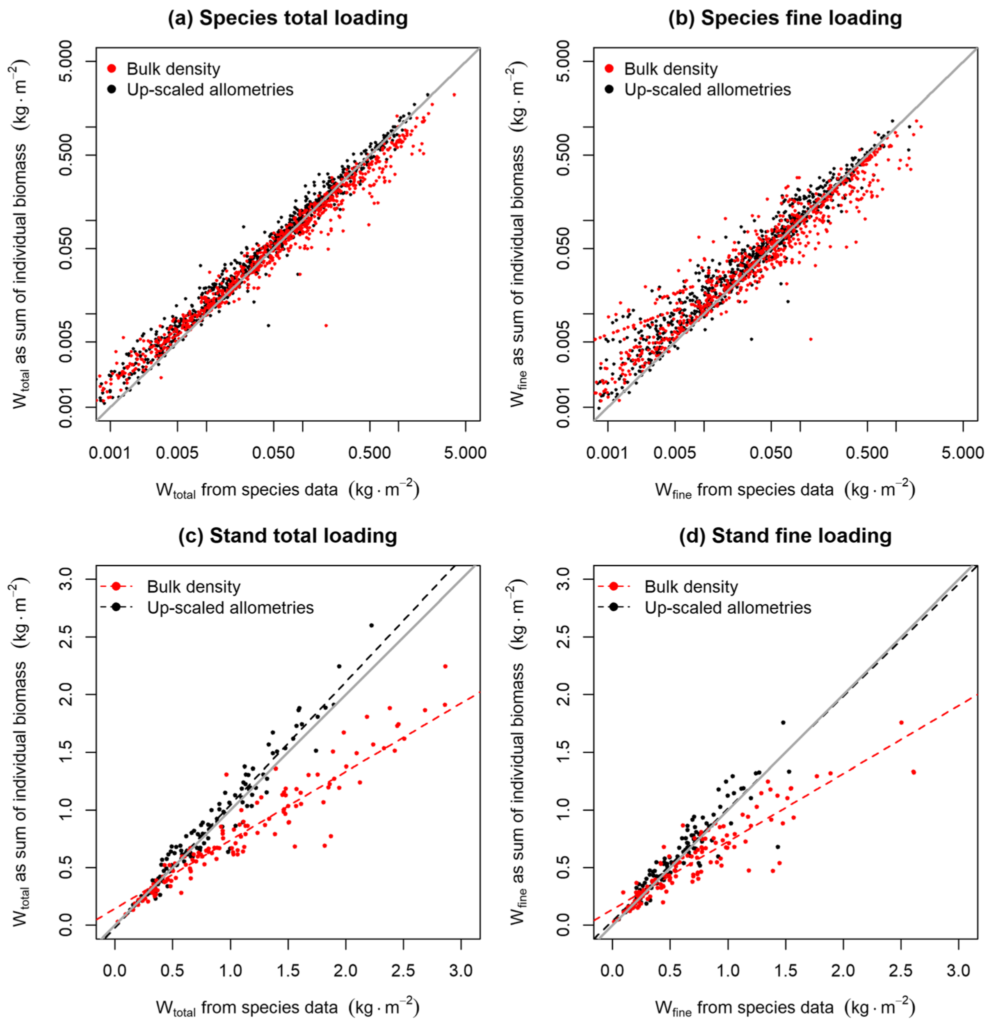

Fig. 3 Comparison of species and stand loadings calculated from species data using either the average bulk density or the proposed approach based on individual-level allometries. Benchmark loadings (*y* axes) are those obtained from aggregation of individual biomass estimates

4 Discussion

Species-specific allometric models developed at individual level are commonly used as an indirect method to predict biomass when destructive techniques are economically (i.e., time consuming) or scientifically (i.e., repeated inventories) limited (Catchpole and Wheeler 1992; Bonham 2013). The individual-level biomass allometries for 26 Mediterranean species presented here complement existing equations for the same or other shrub species in Iberian Peninsula (Pereira et al. 1995; Castro et al. 1996; Paton et al. 2002; Blanco-Oyonarte and Navarro-Cerrillo 2003; Castro and Freitas 2009). Individual-level allometries have potential limitations derived from intra-specific or habitat-specific variations and, accordingly, including location as a factor-improved models of total biomass in five of the nine species where different localities had been sampled. Our study was not designed to test location effects, and it is likely that predictive ability of

Table 3 Predictive performance (mean absolute error [MAE], bias, and coefficient of determination [R^2]) of species loadings calculated using the proposed approach based on individual allometries and species mean height and cover data obtained from either aggregation of individual measurements ("individual sampling + aggregation") or visual estimation (visual species sampling). In all cases, benchmark loadings are those obtained from aggregation of individual biomass estimates ($n = 49$ after aggregation). Brackets for MAE and bias indicate relative values

Fraction	Source of species data	MAE (kg m^{-2}) [%]	Bias (kg m^{-2}) [%]	R^2
Total fuel (W_{total})	Individual sampling + aggregation	0.077 [34.7%]	+ 0.077 [+ 34.4%]	0.950
	Visual species sampling	0.099 [44.8%]	+ 0.068 [+ 30.8%]	0.838
Fine fuel (W_{fine})	Individual sampling + aggregation	0.039 [27.8%]	+ 0.037 [+ 26.8%]	0.966
	Visual species sampling	0.061 [43.8%]	+ 0.038 [+ 27.0%]	0.827

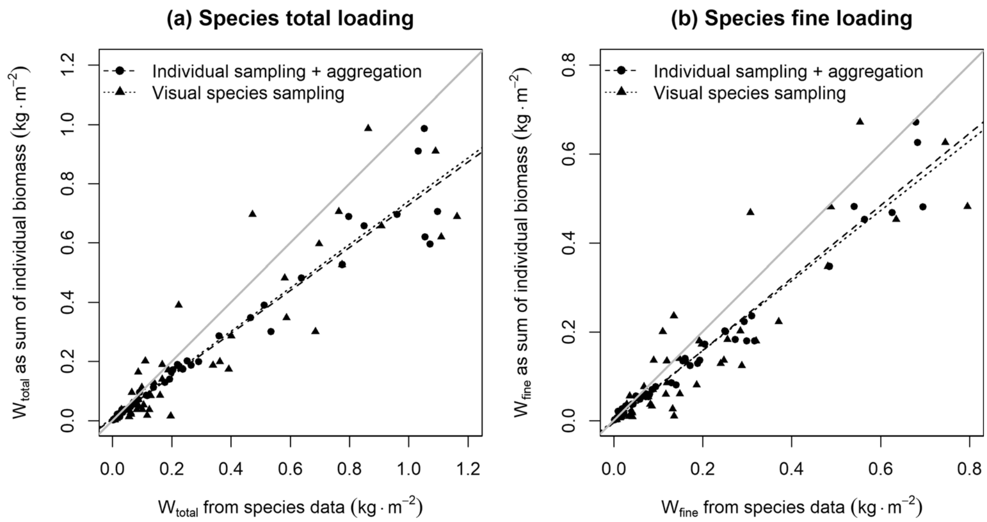

Fig. 4 Comparison of species loadings calculated using species mean height and cover values obtained from either aggregation of individual measurements ("individual sampling + aggregation") or visual estimation ("visual species sampling"). Benchmark loadings (*y* axes) are those obtained from aggregation of individual biomass estimates

allometries would decrease when applied to localities with micro-environmental conditions different from the habitats sampled in this study. Nevertheless, the overall predictive ability of allometries was only slightly better when considering location-specific parameters (Table 1). The precision of allometries decreased strongly (i.e., higher MAE) when calibrated for functional groups in comparison to species-specific allometries, stressing the need to develop species-specific equations.

We presented an approach to apply our (or other) biomass allometries to estimate fuel loading on vegetation data sampled at the species level. Since bulk density (BD) refers to dry weight per unit volume, applications of bulk density values to estimate fuel loading with vegetation sampling at species or stand levels (i.e., arrows "1-2" or "1-3" in Fig. 1) are not uncommon in fire behavior decision support systems (Ottmar et al. 2007). In contrast to allometric equations, using BD assumes that plants have an isometric pattern of development between volume and biomass. Values of $b < 1$ are very frequent in our allometries, indicating that fuel density decreases with volume for most of our studied species. Therefore, using mean BD estimates instead of allometric regressions at the stand level can lead to large errors if the size of plants is different to that of the plants corresponding to the BD value. Our up-scaled use of allometric equations produced more precise (lower MAE) and accurate (lower bias) loading estimates than calculations based on BD. These results were to be expected because allometric equations account for variations in density derived from variations in plant size. We exemplified our method on allometric equations where the predictor for biomass was shrub volume, but the same strategy could be used to up-scale biomass equations based on other plant measurements, such as crown area, diameter, or height (Paton et al. 2002).

Measuring the dimensions of all woody plants in a plot requires much more effort than estimating mean height and percent cover by species. The main advantage of applying individual-level allometric equations to species-level measurements is that it combines relatively fast vegetation sampling (in the application phase) with the possibility to account for variations in BD derived from both species identity and plant size. Empirical relationships between stand vegetation variables and fuel loading also require a low amount of sampling effort in their application phase. Appendix 3 shows the comparison of fuel loading estimates obtained using our proposed method with those obtained using the approaches of Fernandes et al. (2012) and Pasalodos-Tato et al. (2015). Although it requires species identification, the comparison indicates that our approach yields more accurate and precise loading estimates, as it profits from information on species composition within each plot and from allometries calibrated for the target region. Species-specific empirical allometries based on the percent cover and mean height of species in fixed stands are also possible (arrow "2-2" in Fig. 1) (Ruiz-Peinado et al. 2013), but such models require a much larger destructive sampling effort in the development phase compared to individual-level allometries. A further advantage of our approach is that a single individual-based destructive survey is enough to fit fuel and crown area allometries, so that the application to species-level data does not require additional destructive surveys.

Despite its advantages, the proposed method comes with some limitations. First, it requires fitting an additional allometry (height vs. crown area), which for many species we found to be of lower predictive value than biomass allometries (Table 6 Appendix 2). For the worst cases, crown area estimates from allometries would not be better than fixed mean crown area values. Wrong crown area (CA_m) estimates can lead to wrong estimates of shrub volume (V_m) and, hence, poor estimates of biomass $B_{total,m}$ or $B_{fine,m}$. Second, CA_m estimates are also used to derive shrub density from percent cover without accounting for the potential crown overlap between individuals (of the same species/group). Third, our approach involves the assumption that the BD of a shrub of "average" height equals the mean BD of all shrubs of the target species in the vegetation plot. Therefore, we expect the predictive value of our approach to be higher in cases where height of individuals of the target species in the plot is homogeneous. Notwithstanding these weaknesses, which may imply an accumulation of estimation errors, we found that our method reduced the error of loading estimates for most species and species groups with respect to assuming constant BD values (Tables 7 and 8 Appendix 2).

In practical applications of our method, estimates of species mean height and percent cover will be more or less accurate depending on the vegetation sampling method. Our results indicate that an additional 10–16% error should be expected if percent cover and mean height are estimated visually. This increase in error should be evaluated against the benefit of decreasing sampling effort with respect to individual-level measurements. Functions to estimate fuel loading both from individual-level data and from species cover and mean height have been included in the R package "medfuels," which is freely available at GitHub https://github.com/spif-ctfc/medfuels (De Cáceres et al. 2019).

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Data availability The dataset used to develop individual-based allometries has been included in the R package "medfuels," publicly available as a GitHub repository (https://github.com/spif-ctfc/medfuels) and in the Zenodo repository (De Cáceres et al. 2019) at https://doi.org/10.5281/zenodo.3356777. The two datasets used for evaluation of the proposed method are available under request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix 1. Data used to develop individual-level allometries

Our dataset for the development of fuel allometries is a collection of destructive individual-level field data obtained by different research groups aimed to include the most common shrub species in Catalonia while taking into account some of their geographic variation (Appendix Table 4). Specimens of each target species were sampled in one to three locations, depending on the species.

Table 4 Location, vegetation formation, and research group who measured/collected the individual shrub data. Species names in bold italics indicate species that were sampled in more than one location

Location (county)	Species sampled (individuals)	Vegetation formation	Researcher/group
Poblet (Conca de Barberà)	***Quercus ilex*** (15), *Phillyrea latifolia* (15)	Open oak woodland	Marc Taüll
Vilamajor (Montsec)	***Quercus ilex*** (20), ***Q. coccifera*** (20), ***Rosmarinus officinalis*** (20)	Oak shrubland	Marc Taüll
El Perelló (1) (Baix Ebre)	***Quercus coccifera*** (18), ***Rosmarinus officinalis*** (20), *Pistacia lentiscus* (17), *Ulex parviflorus* (20), ***Erica multiflora*** (20)	Open pine woodland	Beatriz Duguy
Trago (Noguera)	***Rosmarinus officinalis*** (50), ***Genista scorpius*** (50)	Open shrubland	Pere Casals
Odèn (Solsonès)	***Buxus sempervirens*** (20), ***Genista scorpius*** (20), *Rosa canina* (20), *Thymus vulgaris* (20)	Encroached grassland	Lluís Coll
Collada de Toses (Cerdanya)	*Cytisus oromediterraneus* (22)	Encroached grassland	Pere Casals
Madrona (Solsonès)	***Buxus sempervirens*** (30), *Viburnum lantana* (30)	Dense pine woodland	SPIF/CTFC
Madrona (Solsonès)	*Ligustrum vulgare* (30), *Cytisophyllum sessilifolium* (30)	Pine forest margin	SPIF/CTFC
Santa Coloma de Farners (La Selva)	*Arbutus unedo* (20), ***Cistus salviifolius*** (20), ***Erica arborea*** (12)	Open pine woodland	SPIF/CTFC
Santa Coloma de Farners (La Selva)	*Erica scoparia* (20), ***Cistus salviifolius*** (20)	Open woodland, dense shrubland	SPIF/CTFC
Sant Celoni (Vallès Oriental)	***Cistus monspeliensis*** (20)	Open pine woodland	SPIF/CTFC
Sant Celoni (Vallès Oriental)	***Erica arborea*** (10), *Viburnum tinus* (20)	Dense pine woodland	SPIF/CTFC
El Perelló (2) (Baix Ebre)	***Erica multiflora*** (10)	Open pine woodland	CTFC
Begues (Baix Llobregat)	*Cistus albidus* (20), ***Erica multiflora*** (20)	Shrubland	SPIF/CTFC
Sant Vicenç dels Horts (Baix Llobregat)	*Spartium junceum* (20)	Shrubland	SPIF/CTFC
Castellbò (Alt Urgell)	*Cistus laurifolius* (20)	Shrubland	CTFC
Can Gorgals (La Selva)	*Lavandula stoechas* (20)	Shrubland	SPIF/CTFC
Can Gorgals (La Selva)	***Cistus monspeliensis*** (10), *Cytisus scoparius* (20)	Open pine woodland	SPIF/CTFC

For each target species present in a sampling site, several individuals (selected to span a range of sizes) were tallied for crown length at its widest point (L_M; cm), the perpendicular crown extent at the same height (L_P; cm) and maximum plant height (H; cm). Each individual was clipped and separated into fine (leaves and < 6 mm diameter stems) and coarse (> 6 mm diameter stems) fuel fractions. Reproductive structures were discarded. Each fraction was weighted in the field (with a precision of 10 and 50 g for fine and coarse fractions, respectively) and a representative subsample was taken to the lab, where it was weighted again after drying in the oven for 48 h at 80 °C. The ratio of fresh weight to dry weight of samples was used to obtain the total dry weight (B_{total}; kg) and the dry weight of fine fuels (B_{fine}; kg) corresponding to each individual. The complete dataset of individual measurements is distributed with package medfuels and is available at Zenodo https://doi.org/10.5281/zenodo.3356777 (De Cáceres et al. 2019).

The projected crown area (CA; cm^2) of each individual was calculated assuming an elliptical crown shape:

$$\mathrm{CA} = \pi \cdot (L_M/2) \cdot (L_P/2) \quad (8)$$

We calculated the apparent shrub volume (V; m^3) using the shape of a cylinder:

$$V = CA \cdot H \quad (9)$$

Bulk density estimates (BD_{fine} and BD_{total}; kg m^{-3}) were obtained dividing the fine or total dry weight by apparent volume and averaged by species and species group. Appendix Table 5 shows the mean and range of the different variables (H, CA, V, B_{fine}, B_{total}, BD_{fine}, and BD_{total}) for individuals of each species.

Table 5 Family, number of individuals (n), number of populations (pop), and mean plant characteristics (minimum and maximum values in brackets) of target species, grouped by life form and post-fire recovery strategy

Species/group	Family	Number	Pop	Height (cm)	Crown area (m^2)	Volume (m^3)	B_{fine} (kg)	B_{total} (kg)	BD_{fine} (kg m^{-3})	BD_{total} (kg m^{-3})
Chamaephytes (Ch)										
Lavandula stoechas L.	Lamiaceae	20	1	82.9 [45, 135]	0.407 [0.031, 1.48]	0.429 [0.02, 1.999]	0.49 [0.07, 1.50]	0.65 [0.07, 2.29]	3.148 [0.407, 20.93]	3.458 [0.815, 20.93]
Thymus vulgaris L.	Lamiaceae	21	1	20.6 [11, 48]	0.119 [0.01, 0.495]	0.034 [0.001, 0.238]		0.23 [0.01, 1.18]		7.937 [4.943, 13.848]
Macro-phanerophytes (MPh)										
Arbutus unedo L.	Ericaceae	20	1	263.3 [90, 500]	2.536 [0.176, 6.465]	8.64 [0.158, 32.327]	1.39 [0.03, 5.00]	4.17 [0.06, 13.90]	0.198 [0.051, 0.328]	0.446 [0.29, 0.81]
Buxus sempervirens L.	Buxaceae	50	2	193.4 [24, 510]	1.546 [0.017, 6.264]	4.763 [0.005, 31.944]	1.12 [0.03, 4.40]	2.34 [0.02, 14.74]	0.232 [0.049, 0.627]	1.352 [0.118, 5.465]
Erica arborea L.	Ericaceae	21	2	200.7 [59, 400]	1.314 [0.118, 6.362]	3.639 [0.089, 25.447]	0.94 [0.02, 4.97]	2.95 [0.07, 21.20]	0.423 [0.024, 2.029]	0.864 [0.323, 2.128]
Ligustrum vulgare L.	Oleaceae	27	1	129.7 [50, 300]	0.374 [0.014, 2.804]	0.739 [0.008, 8.412]	0.09 [0.01, 0.52]	0.21 [0.01, 1.39]	0.281 [0.061, 1.098]	0.446 [0.137, 2.143]
Phillyrea latifolia L.	Oleaceae	15	1	108.3 [57, 150]	0.621 [0.082, 1.858]	0.764 [0.063, 2.731]	0.19 [0.02, 0.61]	0.23 [0.02, 0.62]	0.335 [0.164, 1.023]	0.404 [0.217, 1.023]
Pistacia lentiscus L.	Anacardiaceae	17	1	118.6 [45, 266]	3.384 [0.068, 16.022]	6.061 [0.031, 42.619]	3.26 [0.12, 12.38]	8.41 [0.13, 52.85]	1.339 [0.19, 3.847]	2.220 [1.012, 4.609]
Quercus ilex L.	Fagaceae	33	2	55.1 [16, 102]	0.476 [0.011, 2.112]	0.38 [0.002, 2.053]	0.19 [0.00, 0.98]	0.25 [0.00, 1.29]	1.124 [0.199, 2.657]	1.533 [0.263, 4.104]
Viburnum lantana L.	Adoxaceae	29	1	136.8 [45, 270]	0.597 [0.039, 2.177]	1.114 [0.02, 5.878]	0.11 [0.01, 0.60]	0.27 [0.01, 1.83]	0.286 [0.038, 1.072]	0.439 [0.101, 1.996]
Viburnum tinus L.	Adoxaceae	20	1	212.7 [85, 340]	1.395 [0.255, 5.203]	3.651 [0.217, 16.65]	0.32 [0.04, 1.47]	0.90 [0.06, 4.59]	0.120 [0.04, 0.268]	0.264 [0.095, 0.547]
Nano-phanerophytes (NPh)										
Facultative seeders										
Cytisophyllum sessilifolium (L.) O. Lang	Fabaceae	30	1	63.2 [30, 108]	0.13 [0.011, 0.565]	0.094 [0.003, 0.452]	0.03 [0.00, 0.14]	0.03 [0.00, 0.15]	0.331 [0.154, 0.799]	0.369 [0.154, 0.947]
Cytisus scoparius (L.) Link.	Fabaceae	20	1	205.2 [75, 310]	0.835 [0.11, 2.615]	1.998 [0.082, 7.846]	1.10 [0.16, 4.18]	1.94 [0.40, 6.33]	0.94 [0.197, 5.4]	1.33 [0.582, 5.4]

Table 5 (continued)

Species/group	Family	Number	Pop	Height (cm)	Crown area (m^2)	Volume (m^3)	B_{fine} (kg)	B_{total} (kg)	BD_{fine} (kg m^{-3})	BD_{total} (kg m^{-3})
Erica multiflora L.	Ericaceae	49	3	92.2 [27, 173]	0.584 [0.028, 2.174]	0.605 [0.014, 3.261]	0.75 [0.03, 2.54]	0.90 [0.03, 3.03]	1.648 [0.243, 5.846]	1.889 [0.396, 6.361]
Genista scorpius (L.) DC. in Lam. et DC.	Fabaceae	80	2	53.0 [16, 120]	0.183 [0.009, 2.325]	0.126 [0.003, 2.79]		0.29 [0.01, 5.08]		2.748 [0.101, 21.052]
Spartium junceum L.	Fabaceae	20	1	239.5 [135, 390]	2.565 [0.424, 9.331]	7.435 [0.593, 33.59]	1.93 [0.10, 7.85]	5.33 [0.15, 28.55]	0.28 [0.145, 0.751]	0.721 [0.245, 2.003]
Resprouters										
Cytisus oromediterraneus Ribas mart.	Fabaceae	22	1	64.0 [12, 140]	1.174 [0.012, 4.123]	1.161 [0.004, 5.187]	1.27 [0.02, 5.34]	2.25 [0.02, 9.20]	2.208 [0.65, 8.697]	3.026 [1.39, 9.625]
Erica scoparia L.	Ericaceae	20	1	163.1 [50, 230]	0.721 [0.101, 5.003]	1.382 [0.098, 11.257]	0.65 [0.04, 3.85]	1.36 [0.06, 10.04]	0.597 [0.225, 1.972]	0.973 [0.347, 2.216]
Quercus coccifera L.	Fagaceae	39	2	77.2 [16, 200]	0.708 [0.013, 5.301]	0.893 [0.002, 7.422]	0.32 [0.01, 1.49]	0.47 [0.01, 2.01]	1.854 [0.159, 11.716]	2.372 [0.21, 17.513]
Rosa canina L.	Rosaceae	20	1	126.4 [45, 280]	1.65 [0.038, 8.247]	3.079 [0.027, 23.091]		2.55 [0.03, 18.58]		0.985 [0.392, 2.409]
Seeders										
Cistus albidus L.	Cistaceae	20	1	80.5 [27, 170]	0.294 [0.038, 0.95]	0.311 [0.01, 1.472]	0.115 [0.023, 0.515]	0.20 [0.03, 0.84]	0.836 [0.11, 2.452]	1.154 [0.323, 3.822]
Cistus laurifolius L.	Cistaceae	20	1	102.4 [40, 170]	0.655 [0.018, 2.377]	0.873 [0.009, 3.327]	1.013 [0.031, 3.456]	1.80 [0.03, 5.97]	3.221 [0.246, 15.534]	4.342 [0.246, 23.431]
Cistus monspeliensis L	Cistaceae	20	2	96.5 [40, 168]	0.427 [0.011, 3.063]	0.534 [0.009, 5.146]	0.854 [0.014, 5.738]	1.27 [0.01, 10.67]	3.068 [0.232, 19.012]	3.523 [0.232, 19.012]
Cistus salviifolius L.	Cistaceae	39	2	102.5 [50, 190]	0.809 [0.044, 2.686]	0.927 [0.041, 3.224]	0.288 [0.02, 1.249]	0.37 [0.02, 1.95]	0.373 [0.074, 0.999]	0.443 [0.074, 1.18]
Rosmarinus officinalis L.	Lamiaceae	97	3	63.3 [18, 195]	0.254 [0.003, 2.67]	0.279 [0.001, 4.994]	0.478 [0.01, 1.54]	0.49 [0.00, 4.70]	1.636 [0.445, 3.376]	3.415 [0.737, 13.263]
Ulex parviflorus Pourr.	Fabaceae	20	1	88.9 [37, 123]	0.262 [0.061, 0.761]	0.258 [0.023, 0.936]	0.218 [0.02, 0.55]	0.30 [0.02, 1.00]	0.965 [0.523, 1.573]	1.256 [0.713, 1.867]

Appendix 2. Supplementary Tables

Table 6 Allometric regression coefficients (*a* and *b*) and cross-validated R^2 of the biomass (total and fine fuels) and crown area models fitted for both species and groups. For species, column R^2 *full* indicates the cross-validated R^2 of a model including location as additional predictor (Eq. (3)) and *p-LRT* is the *p* value of a likelihood ratio test between a model without location and a model including it (Eqs. (2) and (3)). For species groups, *p-LRT* and R^2 *full* are the same as before but replacing the role of location by species. Missing values for *p-LRT* and R^2 *full* correspond to cases where either only one location was sampled, the fuel size fractions were not separated in one or more locations, or the species group includes only one species with data

	Total biomass (B_{total})					Fine fuel biomass (B_{fine})					Crown area (*CA*)				
Species/group	a_{total}	b_{total}	R^2	*p-LRT*	R^2 *full*	a_{fine}	b_{fine}	R^2	*p-LRT*	R^2 *full*	a_{area}	b_{area}	R^2	*p-LRT*	R^2 *full*
Chamaephytes (Ch)	1.9189	0.6873	0.77	0.000	0.75	0.7963	0.3762	0.43			24.589	1.1662	0.54	0.000	0.88
Lavandula stoechas L.	1.1574	0.4851	0.70			0.7963	0.3762	0.43			0.0065	2.9626	0.91		
Thymus vulgaris L.	6.6493	0.9605	0.91								0.8229	2.3530	0.50		
Macro-phanerophytes (MPh)	0.7856	0.8101	0.62	0.000	0.91	0.3596	0.7138	0.51	0.000	0.77	5.8458	1.4944	0.36	0.000	0.67
Arbutus unedo L.	0.3973	1.0774	0.89			0.2375	0.8631	0.68			0.6284	1.8804	0.73		
Buxus sempervirens L.	1.0581	0.6849	0.59	0.000	0.62	0.3032	0.7163	0.54			0.9734	1.8072	0.80	0.000	0.81
Erica arborea L.	0.8820	0.9224	0.82	0.213	0.48	0.4234	0.7111	0.70	0.413	0.41	7.5880	1.3760	0.55	0.001	0.69
Ligustrum vulgare L.	0.3225	0.8106	0.80			0.1427	0.6443	0.84			8.0727	1.2580	0.37		
Phillyrea latifolia L.	0.3106	0.7510	0.94			0.2502	0.7300	0.89			0.0080	2.8650	0.35		
Pistacia lentiscus L.	2.1723	0.8654	0.96			1.1897	0.7337	0.74			0.0173	2.9654	0.55		
Quercus ilex L.	0.7327	0.7376	0.83	0.000	0.83	0.5239	0.7337	0.84	0.012	0.81	1.8575	1.8855	0.61	0.000	0.79
Viburnum lanta L.	0.2872	0.7045	0.64			0.1308	0.5352	0.67			0.1068	2.1725	0.72		
Viburnum tinus L.	0.2766	0.9225	0.81			0.1349	0.7261	0.79			9.4880	1.3509	0.30		
Nano-phanerophytes (NPh)	1.2694	0.7610	0.77	0.053	0.74	0.7900	0.6942	0.63	0.060	0.55	0.9843	1.8759	0.43	0.000	0.47
Facultative seeders	1.2832	0.8258	0.79	0.000	0.65	0.7803	0.8240	0.70	0.000	0.66	1.9168	1.6929	0.53	0.000	0.65
Cytisophyllum sessilifolium (L.) O. Lang	0.2313	0.8516	0.74			0.2068	0.8514	0.76			0.3508	1.9641	0.09		
Cytisus scoparius (L.) Link.	1.2729	0.6773	0.89			0.8236	0.5315	0.66			0.0966	2.1168	0.31		
Erica multiflora L.	1.4374	0.7916	0.68	0.181	0.68	1.1799	0.7531	0.50	0.009	0.57	10.171	1.3991	0.13	0.000	0.30
Genista scorpius (L.) DC. in Lam. et DC.	1.9220	0.8807	0.95	0.360	0.95						0.8461	1.8983	0.42	0.000	0.69
Spartium junceum L.	0.5981	1.1340	0.54			0.2683	1.0322	0.63			0.1543	2.1752	0.30		
Resprouters	1.2405	0.7436	0.77	0.000	0.93	0.7898	0.6622	0.56	0.000	0.86	3.5246	1.6961	0.29	0.000	0.54
Cytisus oromediterraneus Ribas mart.	2.1591	0.8257	0.97			1.3856	0.7712	0.84			1.2410	2.1042	0.84		
Erica scoparia L.	0.9959	1.0594	0.92			0.5492	0.8479	0.86			30.709	1.0000	0.07		
Quercus coccifera L.	0.7559	0.5713	0.73	0.180	0.73	0.5148	0.5312	0.79	0.077	0.78	0.1306	2.4084	0.27	0.092	0.21
Rosa canina L.	0.9742	0.9396	0.95								11.157	1.4713	0.69		
Seeders	1.2796	0.7270	0.52	0.000	0.78	0.7777	0.6476	0.45	0.000	0.75	0.1376	2.2836	0.48	0.000	0.55
Cistus albidus L.	0.4841	0.6330	0.68			0.2435	0.4986	0.36			0.6035	1.9060	0.46		
Cistus laurifolius L.	2.3847	0.7004	0.77			1.3792	0.6066	0.74			0.0003	3.5744	0.53		
Cistus monspeliensis L	2.3232	0.7917	0.85	0.000	0.83	1.6252	0.6947	0.74	0.000	0.75	0.0700	2.3642	0.25	0.001	0.29
Cistus salviifolius L.	0.4032	0.8618	0.56	0.000	0.87	0.3211	0.7940	0.59	0.000	0.86	1.9952	1.7842	0.27	0.001	0.33
Rosmarinus officinalis L.	1.9918	0.8348	0.82	0.002	0.71	1.3196	0.8929	0.77	0.001	0.82	0.1544	2.2532	0.51	0.000	0.54
Ulex parviflorus Pourr.	1.1109	0.9279	0.80			0.7171	0.8293	0.68			1.9095	1.6006	0.42		

Table 7 Number of species records (n) corresponding to each species/group and mean absolute error (kg/m^2) of species loadings calculated using either the average bulk density or the proposed method based on individual-level allometries. In all cases, benchmark loadings are those obtained from aggregation of individual biomass. Rows of species groups correspond to those species records for which a species-specific allometry is missing

		Fine fuel loading			Total fuel loading		
Species/group	*n*	Bulk density	Up-scaled allometries	Diff.	Bulk density	Up-scaled allometries	Diff.
Chamaephytes (Ch)	116	0.0295	0.0280	− 0.0016	0.0125	0.0117	− 0.0009
Lavandula stoechas L.	1	0.0052	0.0031	− 0.0021	0.0042	0.0023	− 0.0018
Thymus vulgaris L.	33	0.0008	0.0010	0.0002	0.0008	0.0010	0.0002
Macro-phanerophytes (MPh)	116	0.0152	0.0067	− 0.0085	0.0201	0.0096	− 0.0106
Arbutus unedo L.	4	0.0017	0.0011	−0.0006	0.0020	0.0013	− 0.0008
Buxus sempervirens L.	29	0.0232	0.0088	− 0.0144	0.0594	0.0338	− 0.0256
Erica arborea L.	1	0.0201	0.0070	− 0.0131	0.0094	0.0022	− 0.0071
Phillyrea latifolia L.	6	0.0016	0.0038	0.0022	0.0018	0.0042	0.0025
Pistacia lentiscus L.	36	0.0118	0.0176	0.0058	0.0116	0.0149	0.0033
Quercus ilex L.	8	0.0355	0.0126	− 0.0228	0.0477	0.0176	− 0.0301
Nano-phanerophytes (NPh)	29	0.0326	0.0251	− 0.0074	0.0546	0.0342	− 0.0204
Facultative seeders	23	0.0019	0.0027	0.0008	0.0031	0.0044	0.0013
Cytisophyllum sessilifolium (L.) O. Lang	1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Erica multiflora L.	30	0.0188	0.0124	− 0.0064	0.0183	0.0116	− 0.0067
Genista scorpius (L.) DC. in Lam. et DC.	77	0.0155	0.0054	− 0.0100	0.0155	0.0054	− 0.0100
Spartium junceum L.	1	0.0001	0.0000	− 0.0001	0.0013	0.0001	− 0.0013
Resprouters	70	0.0195	0.0103	− 0.0092	0.0165	0.0109	− 0.0057
Cytisus oromediterraneus Ribas mart.	12	0.0681	0.0502	− 0.0179	0.0698	0.0561	− 0.0137
Erica scoparia L.	1	0.0108	0.0002	− 0.0106	0.0075	0.0002	− 0.0073
Quercus coccifera L.	78	0.1866	0.0376	− 0.1490	0.2227	0.0480	− 0.1746
Rosa canina L.	12	0.0066	0.0071	0.0006	0.0066	0.0071	0.0006
Seeders	20	0.0073	0.0031	− 0.0042	0.0041	0.0030	− 0.0011
Cistus albidus L.	14	0.0024	0.0032	0.0008	0.0023	0.0029	0.0006
Cistus monspeliensis L	3	0.0026	0.0017	− 0.0009	0.0019	0.0012	− 0.0007
Cistus salviifolius L.	4	0.0006	0.0003	− 0.0003	0.0004	0.0002	− 0.0002
Rosmarinus officinalis L.	83	0.0460	0.0224	− 0.0236	0.1912	0.0324	− 0.1588
Ulex parviflorus Pourr.	17	0.0098	0.0072	− 0.0026	0.0103	0.0089	− 0.0014

Table 8 Number of species records (n) corresponding to each species/group and relative mean absolute error (%) of species loadings calculated using either the average bulk density or the proposed method based on individual-level allometries. In all cases, benchmark loadings are those obtained from aggregation of individual biomass. Rows of species groups correspond to those species records for which a species-specific allometry is missing

		Fine fuel loading			Total fuel loading		
Species/group	n	Bulk density	Up-scaled allometries	Diff.	Bulk density	Up-scaled allometries	Diff.
Chamaephytes (Ch)	116	58.4	55.3	− 3.1	30.4	28.4	− 2.1
Lavandula stoechas L.	1	80.6	48.4	− 32.2	75.2	42.1	− 33.1
Thymus vulgaris L.	33	2.2	2.6	0.5	2.2	2.6	0.5
Macro-phanerophytes (MPh)	116	41.1	18.1	− 23.0	25.1	11.9	− 13.2
Arbutus unedo L.	4	9.4	6.2	− 3.2	5.7	3.6	− 2.2
Buxus sempervirens L.	29	30.0	11.3	− 18.7	21.6	12.3	− 9.3
Erica arborea L.	1	46.4	16.2	− 30.2	16.4	3.9	− 12.6
Phillyrea latifolia L.	6	18.1	42.3	24.3	16.2	38.7	22.5
Pistacia lentiscus L.	36	14.9	22.1	7.3	9.1	11.7	2.6
Quercus ilex L.	8	159.9	57.0	− 102.9	154.1	56.8	− 97.3
Nano-phanerophytes (NPh)	29	29.3	22.6	− 6.7	33.0	20.7	− 12.3
Facultative seeders	23	9.6	13.8	4.2	9.6	13.7	4.1
Cytisophyllum sessilifolium (L.) O. Lang	1	34.9	17.2	− 17.7	34.9	17.2	− 17.8
Erica multiflora L.	30	19.5	12.8	− 6.7	16.6	10.5	− 6.0
Genista scorpius (L.) DC. in Lam. et DC.	77	17.1	6.0	− 11.1	17.1	6.0	− 11.1
Spartium junceum L.	1	12.7	1.0	− 11.7	65.5	4.2	− 61.3
Resprouters	70	45.4	23.9	− 21.5	27.8	18.3	− 9.5
Cytisus oromediterraneus Ribas mart.	12	23.2	17.1	− 6.1	16.4	13.2	− 3.2
Erica scoparia L.	1	9.9	0.2	− 9.7	4.9	0.1	− 4.8
Quercus coccifera L.	78	140.9	28.4	− 112.5	120.0	25.9	− 94.1
Rosa canina L.	12	4.9	5.3	0.4	4.9	5.3	0.4
Seeders	20	31.5	13.4	− 18.1	13.7	10.1	− 3.7
Cistus albidus L.	14	24.6	32.8	8.1	18.4	22.9	4.5
Cistus monspeliensis L	3	39.3	25.8	− 13.6	29.3	18.1	− 11.2
Cistus salviifolius L.	4	44.0	21.9	− 22.1	32.4	15.1	− 17.3
Rosmarinus officinalis L.	83	18.5	9.0	− 9.5	45.8	7.8	− 38.0
Ulex parviflorus Pourr.	17	43.2	31.9	− 11.4	34.5	29.9	− 4.7

Appendix 3. Comparison of alternative loading estimation models

We compared the performance of our proposed method of shrub loading estimation from species-level vegetation data with the approaches of Fernandes et al. (2012) and Pasalodos-Tato et al. (2015), both requiring stand-level vegetation estimates. To apply these alternative approaches, we aggregated individual-level data of the 131 10 × 10-m plots into stand-level estimates of percent cover (C; in %) and mean height (H_m; in m) in the same way as we did to obtain species-level data (for nine plots C exceeded 100% and had to be truncated). Fernandes et al. (2012) provide the following equation to estimate shrub fine fuel loading, based on Fernandes et al. (2002):

$$W_{fine} = 0.555 \cdot (C \cdot H_m)^{0.743} \tag{10}$$

Pasalodos-Tato et al. (2015) provide the following equation to estimate shrub total loading:

$$W_{total} = a_0 + a_1 \cdot ln(H_m) + a_2 \cdot ln(FCC_{Bliss}) \tag{11.1}$$

where FCC_{Bliss} is the so-called Bliss transformation of shrub percentage cover:

$$FCC_{Bliss} = sin^{-1}\left(\sqrt{C/100}\right) \tag{11.2}$$

Pasalodos-Tato et al. (2015) provide a_0, a_1, and a_2 parameter values for several habitats of Andalusia (S of Spain). We classified the 131 field plots into habitat classes, according to the Map of Catalan Habitats (1:50,000) based on the review and adaptation to the Catalan territory to the EU List of Habitats of Community Interest (Carreras et al. 2016). Comparing the Catalan habitat definitions and the Andalusian habitat descriptions in Pasalodos-Tato et al. (2015), we could establish a correspondence for 95 plots, corresponding to five different Andalusian habitats (see Appendix Table 9).

We compared the predictive value of the fine fuel loading estimates of our approach based on species-level data with those obtained by applying Fernandes et al. (2012) on the set of 131 plots. Similarly, we compared the total loading estimates of our approach with those obtained applying Pasalodos-Tato et al. (2015) on the 95 for which a habitat correspondence could be established.

Table 9 Number of field plots (*n*) classified into Catalan habitat map classes, their corresponding CORINE code and Andalusian habitat formation, description and regression coefficients (a_0, a_1 and a_2) provided by Pasalodos-Tato et al. (2015)

Number	Catalan habitat map unit[a]	CORINE code[b]	Formation[c]	Andalusian habitat description[c]	a_0	a_1	a_2
32	32 t	32.41	170	Associations dominated by Kernes oak	− 0.483	1.347	1.174
16	32 h	32.123/32.211/32.214/ 32.2191/32.24	180	Thicket of mastic trees	− 0.483	1.347	1.174
44	32k/32ab/32l/32u	32.321*/32.322*/32.42/32.431/32.433 32.4B/32.4E	210	Heathers, *Erinaceae* bushes and related groups	0.503	1.060	1.581
1	32x/32n	32.432/32.348/32.36/32.4 J	220a	Rockrose shrubs and *Cistaceae* bushes	2.586	0.000	1.715
2	32w/32n/32u	32.4811*/32.374*/32.375*/32.379*/32.4H	240	Leguminous gorse shrubs and related groups	0.737	0.811	1.189

[a] Map of Catalan Habitats (Carreras et al. 2016)

[b] Directive 79/409/EEC

[c] Pasalodos-Tato et al. (2015)

As before, we evaluated each approach by calculating bias, mean absolute error (MAE), and coefficient of determination (R^2) of the stand loading estimates with respect to the benchmark values, which again were loadings obtained from aggregation of individual biomass estimates. The results of the comparison are shown in Appendix Table 10 and Appendix Fig. 5. Estimates provided by the equation of Fernandes et al. (2012) most often overestimated fine fuel loading, resulting in a much larger bias and MAE compared to our approach. A possible explanation of this divergence could be that the equation of Fernandes et al. (2002) was calibrated using data from understory species in *Pinus pinaster* Ait. forests, where climate is wetter than our study area and hence could support species with larger bulk density such as *Erica* spp. and *Ulex europaeus*.

Table 10 Predictive performance (mean absolute error [MAE], bias, and coefficient of determination [R^2]) of loadings calculated from species data using the proposed method or from stand-level data using the approaches of Fernandes et al. (2012) or Pasalodos-Tato et al. (2015). In all cases, benchmark loadings are those obtained from aggregation of individual biomass. Brackets for MAE and bias indicate relative values

Fraction	Method	Number	MAE (kg m^{-2}) [%]	Bias (kg m^{-2}) [%]	R^2
Fine fuel (W_{fine})	This study	131	0.074 [13.7%]	− 0.025 [− 4.6%]	0.879
	Fernandes et al. (2012)	131	0.526 [78.8%]	+ 0.418 [+ 77.3%]	0.601
Total fuel (W_{total})	This study	95	0.083 [10.2%]	− 0.036 [− 4.5%]	0.951
	Pasalodos-Tato et al. (2015)	95	0.275 [33.8%]	+ 0.102 [+ 12.5%]	0.696

Total fuel loadings obtained using Pasalodos-Tato et al. (2015) had better predictive capacity compared to Fernandes et al. (2012), probably because climatic conditions are closer to those of our study region and the use of habitat-specific equations (Appendix Table 10; Appendix Fig. 5b). Still, their estimates had lower precision (higher MAE) and larger bias than the estimates obtained using our approach. Here, the divergence can be explained by uncertainties in the correspondence between Catalan and Andalusian habitats, but also to the fact that our approach accommodates better to the variation of species composition among plots assigned to the same habitat.

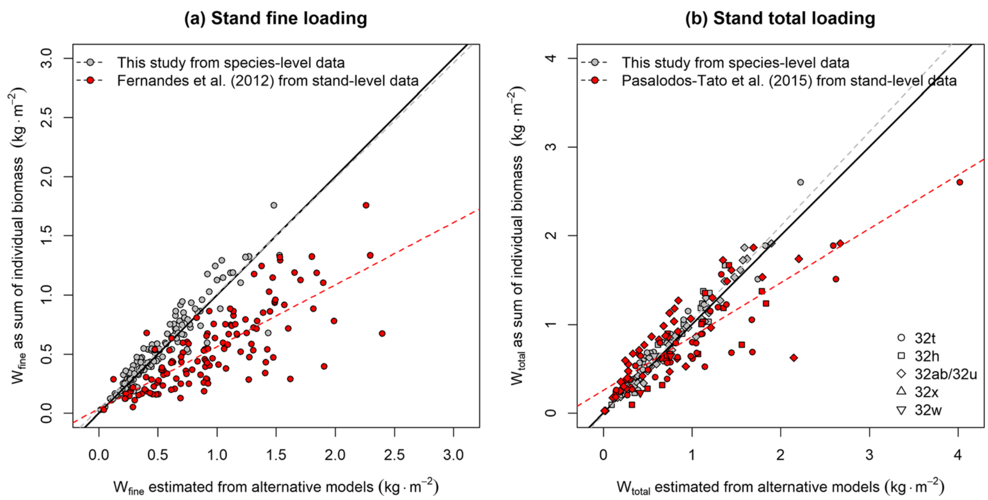

Fig. 5 Comparison of loadings calculated from species data using the proposed method or from stand-level data using the approaches of Fernandes et al. (2012) or Pasalodos-Tato et al. (2015). Benchmark loadings (*y* axis) are those obtained from aggregation of individual biomass

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