Plant Soil (2026) 522:1439–1453
https://doi.org/10.1007/s11104-026-08584-7

RESEARCH ARTICLE

Carbon allocation traits are coordinated across plant organs, yet dry matter content is decoupled in three Mediterranean woody species

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Received: 4 March 2026 / Accepted: 14 April 2026 / Published online: 1 May 2026
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Abstract

Background and aims Trait-based functional ecology often assumes that plant organs (e.g. leaf, stem, root) having dense tissues (high dry matter content; DMC) are carbon (C)-expensive. However, this assumption remains largely untested. Here, we examine whether 1) C-allocation traits co-vary forming coordinated functional strategies, 2) isotopic composition of leaf carbon ($\delta^{13}C$) can be effectively traced across organs and can estimate C present in upper soil layers thereby forming a plant-soil continuum, and 3) easy-to-collect traits can predict key soil ecosystem functions (C stock, nutrient status).

Methods We focused on three widely distributed Mediterranean woody species (*Cistus salviifolius, Erica arborea, Quercus ilex*), measuring plant traits and soil parameters from three sites in Italy. We applied a Bayesian analytical framework considering the co-varying effects of biotic (species, developmental stage) and abiotic (site, fire disturbance) factors.

Results Trait co-variation indicates integrated functional strategies for C allocation, especially for $\delta^{13}C$ across organs. However, DMC of different organs is decoupled from %C and $\delta^{13}C$ of the relative organ.

Responsible Editor: Hans Lambers.

Silvia Portarena and Angelino Carta share senior authorship.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s11104-026-08584-7.

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We find no evidence for the occurrence of a $\delta^{13}C$ plant-soil continuum, nor for easy-to-collect traits to predict soil functions.

Conclusion The widely assumed positive relationship between DMC and C investment does not emerge in the three focal Mediterranean woody species, suggesting within-organ water content regulation as a key morpho-physiological adjustment in our model system. While the focal species are representative of the phylogenetic and functional variation in the Mediterranean woody flora, the generality of our findings should be tested in other regions hosting mediterranean-type ecosystems.

Keywords Carbon cycling · Functional decoupling · Ontogeny · Plant-soil interactions · Soil carbon stock · Trait coordination

Introduction

The study of biomass allocation strategies constitutes a key research topic in plant functional ecology (e.g. Givnish 1986; Castorena et al. 2022). For example, it is widely assumed that denser plant tissues, such as sclerophyllous leaves, are more resource-expensive in terms of carbon (C) allocated to different organs. Consistent evidence shows how organ lifespan is positively correlated to its dry matter content (DMC) across organizational levels and spatial scales (e.g. Wright et al. 2002; Reich et al. 2003; Kitajima and Poorter 2010) – as in the case of leaf dry matter content (LDMC) and leaf lifespan for non-succulent species. In other words, there is a tendency to assume that plants having denser and longer-lived leaves (resource-conservative) are more "C-expensive" than less dense, shorter-lived and "C-cheaper" leaves (resource-exploitative). However, C is not necessarily a limiting factor to plant growth, especially in open ecosystems – such as open woodlands, garrigues, savannas, temperate grasslands – where light availability is abundant. It remains therefore questionable, and largely untested, why a coupling between organ tissue density (e.g. DMC) and C allocation (e.g. %C) should occur in different plant organs.

In plants, C-allocation traits can, or are expected to, serve as indicators of C investments into different organs (e.g. %C, DMC) as well as into growth (e.g. stem diameter, plant height). Plant strategies – identified by bivariate or multivariate trait co-variation forming coordinated functional syndromes (Westoby et al. 2002; Reich et al. 2003; Midolo et al. 2024; Ottaviani et al. 2025, 2026a) – are shaped by plant evolutionary history as well as by environmental conditions (e.g. Kazakou et al. 2006; Fortunel et al. 2009; Ciccarelli et al. 2023; Cruz-Tejada et al. 2024; Dai et al. 2025) and may vary among different growth or life forms (e.g. Ottaviani et al. 2022, 2025). Plant functional traits can respond to changing environments and these changes may then cascade and impact ecosystem functioning (Lavorel and Garnier 2002; Violle et al. 2007). For example, LDMC can vary predictably with increasing aridity, such that higher LDMC values are recorded in non-succulent species (Kazakou et al. 2006; Fortunel et al. 2009; Ottaviani and Keppel 2018). This morpho-physiological adjustment can, in turn, scale up and alter litter quality and decomposition rate as well as flammability at the ecosystem level (Fortunel et al. 2009; Cornelissen et al. 2017; Alam et al. 2025; Schneider et al. 2026). It is therefore justified to consider DMC traits as predictors of specific ecosystem functions, e.g. biogeochemical cycles (Garnier et al. 2004; Hodgson et al. 2011; Pakeman et al. 2011). However, the identification of a set of quick- and easy-to-collect traits that can reliably and consistently estimate relevant ecosystem functions – such as to readily predict soil C stock and nutrient status – remains elusive. This challenge limits our ability to connect aboveground plant strategies with belowground C dynamics, especially under changing climatic conditions (Bardgett et al. 2014; Ottaviani et al. 2021; Klimešová et al. 2023).

In terms of flow, C is absorbed by plants in leaves during photosynthesis and then translocated to different plant organs. Such C flow can be traced by stable carbon isotopic composition ($\delta^{13}C$) which provides a

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reliable proxy to track C allocation across organs (e.g. stems, roots) and assists the evaluation of how plants distribute the assimilated C in response to biotic and abiotic factors. During CO_2 fixation, Rubisco discriminates against the heavier ^{13}C, preferentially incorporating ^{12}C into photosynthetic products (Farquhar et al. 1989). Under high-temperature and water-scarcity conditions, which typically define mediterranean-type climates (Cowling et al. 1996), plants tend to limit their stomata openness to conserve water, the intercellular CO_2 concentration decreases, reducing the substrate pool available for Rubisco discrimination resulting in less negative $\delta^{13}C$ values in plant tissues (Cernusak et al. 2013; Alon et al. 2024; Portarena et al. 2025). Therefore, during warm and dry seasons, plants modulate gas exchanges by coordinated morpho-physiological strategies. These include tight stomata regulation (Farquhar et al. 1989; Hultine and Marshall 2000; Cernusak et al. 2013), high stomatal density and small stomata in conjunction with less negative turgor loss point (Alon et al. 2024) as well as having pubescent leaves (e.g. Ehleringer 1982). Furthermore, part of this $\delta^{13}C$ signal may be translocated to the soil, e.g. through root exudates or mycorrhizal associations and networks (Pickles et al. 2017; de Tombeur et al. 2021; Scartazza et al. 2023) or leaf shedding (Garnier et al. 2004; Kazakou et al. 2006; Fortunel et al. 2009; Cornelissen et al. 2017). However, the existence of such a plant-soil continuum for C-allocation strategies is poorly examined, especially in mediterranean-type ecosystems.

Here, we set out to start filling these knowledge gaps, which constitute our main research goals. We focus on three locally abundant and widely distributed Mediterranean woody species (*Cistus salviifolius*, *Erica arborea*, *Quercus ilex*) at three sites in Italy. These species differ in their post-fire strategies (the reseeder *C. salviifolius* vs the resprouter *E. arborea* and *Q. ilex*), leaf habit (the needle-like *E. arborea* vs broadleaved *C. salviifolius* and *Q. ilex*), longevity and growth forms (Ottaviani et al. 2026a) – offering a suitable model as they are representative of the phylogenetic and functional variation of Mediterranean woody flora. In this Mediterranean case study, we test three hypotheses by modelling trait coordination and accounting for the structuring effect on trait covariation of biotic and abiotic factors related to species identity, individual developmental stage as well as within- and among-site variability.

H1: C-allocation traits co-vary forming coordinated functional strategies.
We explore whether DMC of leaves, stems and belowground coarse organs (thick roots, lignotubers) is coupled with the percentage of C allocated to the respective organ, and if there is a relationship between C-allocation traits of different organs and aboveground plant growth (i.e. basal stem diameter, canopy occupancy). We also examine if DMC reliably reflects plant water- use efficiency – as expected from its proposed correlation with $\delta^{13}C$ – which may constitute a key morpho-physiological functional strategy allowing plants to cope with the warm and dry Summers defining the mediterranean-type climate.

H2: A plant-soil continuum occurs for $\delta^{13}C$.
We test whether the three focal Mediterranean woody species exhibit a plant-soil continuum in C allocation, namely if the carbon absorbed in the leaves can be traced in the stems, belowground coarse organs (lignotubers, thick roots) down to the upper soil layer – highlighted by a tight covariation between $\delta^{13}C$ in the leaf, stem, belowground organs and soil.

H3: Easy-to-collect C-allocation plant traits can predict key soil ecosystem functions.
We examine whether two fundamental ecosystem functions for climate change policies – i.e. C stock (%C) and nutrient status (estimated via carbon to nitrogen ratio, C/N) of the upper soil layer (~5cm deep) – can be assessed by a few easy- and quick-to-collect aboveground C-allocation traits (basal stem diameter, DMC of stems or leaves).

Materials and methods

Study sites

We worked on three study sites in Italy, Mediterranean Basin, experiencing high seasonality defined by xeric Summers (warm and dry) and mesic Winters (cool and wet): Montiferru (geographic centroid: 40.1662048823 N, 8.6397768366 E), Mt Morrone (geographic centroid: 42.1005229667 N, 13.9231161

E), Mt Pisano (geographic centroid: 43.7288732109 N, 10.5761829773 E). Within each site, we identified sampling areas by stratifying for main abiotic variables (i.e. elevation, aspect, slope, bedrock type) to reduce within-site environmental heterogeneity. Montiferru and Mt Pisano sites are on silica-rich soils, whereas Mt Morrone site is on carbonate-rich soils. Because fire acts as an eco-evolutionary force shaping plant species' traits and distribution in the Mediterranean Basin (e.g. Pausas and Verdú 2005), we considered the effect of fire regime on trait coordination. As a metric of fire regime, we used the number of fires since the year 1970 (Nfires) that in the study sites proved to be highly collinear with other fire regime metrics (fire return interval, time since last fire; Ottaviani et al. 2026a). Within each site, we selected one sampling area (constituted by a circular plot of ~ 300m^2) corresponding to a specific Nfires (0–3).

Focal plant species and field sampling

We focused on three woody species belonging to three families: *Cistus salviifolius* L. (Cistaceae), *Erica arborea* L. (Ericaceae), *Quercus ilex* L. (Fagaceae). These are habitat-characteristic species and occupy a broad geographic range in the Mediterranean Basin, so constituting good model species indicative of different vegetation types in the study region – also representing well the phylogenetic and functional variation of Mediterranean woody flora. The three species belong to two life-history strategies (especially relevant for post-fire dynamics), namely two resprouters (*E. arborea, Q. ilex*) and one reseeder (*C. salviifolius*).

We conducted the fieldwork activity to collect plant traits and soil parameters during late Spring/early Summer 2024, corresponding to the vegetative and flowering peak in the study sites. We replicated the same sampling design across the three sites. Within each sampling area, we collected data from five to ten individuals for each focal species, depending on species' local occurrence and abundance (Ottaviani et al. 2026a). Overall, we sampled 120 individual plants: 40 *E. arborea*, 50 *Q. ilex,* 30 *C. salviifolius*. On these plants, we measured eleven functional traits reflecting C-allocation strategies. Trait collection followed standardized protocols provided in handbooks (Cornelissen et al. 2003; Wigley et al. 2020) and in other scientific manuscripts (Ottaviani et al. 2022, 2026a; Millan et al. 2024). Among the selected C-allocation traits, only basal stem diameter (stem_diam) and canopy diameter of the entire individual (can_diam) were measured in the field (Table 1). In the field, we also recorded two architectural traits indicative of the developmental stage of each sampled individual (Wigley et al. 2020; Laurans et al. 2024; Millan et al. 2024): number of successive forks (Nforks) for large shrubs and trees (*E. arborea* L. and *Q. ilex*) and number of stems emerging from the ground (Nstems) for small shrubs (*C. salviifolius*). From each individual, we collected 5–10 undamaged leaves, a 1–2 cm long core from the stem base and belowground coarse organ (in both cases removing the bark) by either using a trephor or cutting part of the organ with a saw. Fresh mass weight of plant material (needed for DMC calculation of different organs – see below) was measured using a balance. At the same location of each sampled plant individual, we collected soil material from the upper soil layer (~ 5 cm deep) to measure the two selected soil parameters indicative of two key ecosystem functions, namely % of organic C (soilC; proxy for C stock in the upper soil layer), ratio between C and N (soilCN; proxy for nutrient status of the upper soil layer).

Lab procedures

Of the eleven C-allocation traits, nine (Table 1) – collected from leaves, stems, belowground coarse organs (lignotuber for the resprouter *E. arborea* L. and *Q. ilex*; thick root for the reseeder *C. salviifolius*) – were measured in the lab. We oven-dried the field-collected plant material (at 60 °C for 72 h or at 45 °C until constant weight) and then we processed those samples to measure DMC (expressed as the ratio between oven-dried and fresh mass weight) as well as the concentration and isotopic composition of C (dry mass basis, %C; δ^{13}C) in the different organs (Table 1). For plant C stoichiometric analyses, we ground samples of oven-dried leaves, stems and belowground coarse organs into a fine powder; we then analyzed ~ 0.5 mg aliquots for %C and δ^{13}C using an elemental analyzer (PYROcube, Elementar Analysensysteme GmbH, Langenselbold, Germany) coupled to an Isotope Ratio Mass Spectrometer (Isoprime precision, Elementar UK Ltd, Manchester, UK). We scale-normalized the δ^{13}C values to IAEA international standards, as follows:

Table 1 The eleven plant functional traits informing on C-allocation strategies and the two architectural traits (informing on individual's ontogeny), with their acronym and a brief description of the procedure implemented to sample and measure the trait

TRAIT	ACRONYM (units)	SAMPLING & MEASURING PROCEDURE
C-allocation traits		
Canopy diameter of the entire individual	can_diam (cm)	Diameter (average of the two main dimensions) measured using a meter tape
Basal stem diameter	stem_diam (cm)	Diameter of the main stem at its base measured using a caliper or a meter tape
Leaf dry matter content	LDMC (mg g^{-1})	Ratio between the oven-dried mass (at 60 °C for 72 h) and the fresh mass of 5–10 undamaged leaves per sampled individual
Stem dry matter content	SDMC (mg g^{-1})	Ratio between the oven-dried mass (at 60 °C for 72 h) and the fresh mass of the main stem sampled at its base
Belowground coarse organ dry matter content	BDMC (mg g^{-1})	Ratio between the oven-dried mass (at 60 °C for 72 h) and the fresh mass of the belowground coarse organ sampled a few centimeters below the soil surface
Leaf $\delta^{13}C$	leaf_d13C (‰ VPDB)	Oven-dried (at 45 °C until constant weight) and finely ground leaf samples (collected from 5–10 undamaged leaves), analyzed with an Elemental Analyzer coupled to an Isotope Ratio Mass Spectrometer, scale-normalized following the IAEA international standards
Stem $\delta^{13}C$	stem_d13C (‰ VPDB)	Oven-dried (at 45 °C until constant weight) and finely ground stem samples (collected from the main stem base), analyzed with an Elemental Analyzer coupled to an Isotope Ratio Mass Spectrometer, scale-normalized following the IAEA international standards
Belowground coarse organ $\delta^{13}C$	below_d13C (‰ VPDB)	Oven-dried (at 45 °C until constant weight) and finely ground belowground coarse organ samples (collected a few centimeters below the soil surface), analyzed with an Elemental analyzer coupled to an isotope ratio mass Spectrometer, scale-normalized following the IAEA international standards
Leaf C percentage	leafC (%)	Oven-dried (at 45 °C until constant weight) and finely ground leaf samples (collected from 5–10 undamaged leaves), analyzed using an Elemental Analyzer coupled to an Isotope Ratio Mass Spectrometer, expressed as % of dry mass
Stem C percentage	stemC (%)	Oven-dried (at 45 °C until constant weight) and finely ground stem samples (collected from the main stem base), analyzed with an Elemental Analyzer coupled to an Isotope Ratio Mass Spectrometer, expressed as % of dry mass
Belowground coarse organ C percentage	belowC (%)	Oven-dried (at 45 °C until constant weight) and finely ground belowground coarse organ samples (collected a few centimeters below the soil surface), analyzed using an Elemental Analyzer coupled to an Isotope Ratio Mass Spectrometer, expressed as % of dry mass
Architectural traits (developmental stage)		
Number of stem rank	Nstems (#)	Number of stems emerging from the ground (e.g. from the lignotuber), transformed as rank variable: 1 = 1 stem, 2 = 2–3 stems, 3 = 4–5 stems, 4 = 6–10 stems, 5 = 10+ stems
Number of successive forks	Nforks (#)	Number of successive forks along the main branched structure

$$\delta^{13}C(‰) = (R_s - R_{std})/R_{std} \times 1000 \quad (1)$$

where R_s is the isotope ratio of the sample and R_{std} is the isotope ratio of the international standard. For the calibration of $\delta^{13}C$ measurements, we used IAEA-CH-7 Polyethylene Foil ($\delta^{13}C = -32.15‰$), IAEA-CH6 sucrose ($\delta^{13}C = -10.43‰$), and IAEA-600 caffeine ($\delta^{13}C = -27.5‰$) scaling to the Vienna Pee Dee Belemnite (VPDB) international standard.

For soil analyses, we prepared samples by sieving (2 mm), removing roots, and oven-drying them at 45 °C until constant weight, then grinding the samples into a fine powder. A fraction of soil was treated with 10% hydrochloric acid to remove carbonates (Midwood and Boutton 1998). We analyzed ~ 0.5 mg of soil for C content (expressed as % of dry mass) and $\delta^{13}C$. We analyzed another fraction of untreated soil powder (~ 2 mg) for N content (% dry mass). We determined C and N contents (calculating their ratio) and $\delta^{13}C$ in the soil using an elemental analyzer (PYROcube, Elementar Analysensysteme GmbH, Langenselbold, Germany) coupled to an Isotope Ratio Mass Spectrometer (Isoprime precision, Elementar UK Ltd, Manchester, UK). We calculated soil $\delta^{13}C$ following the same procedure and *Eq.* 1 reported above for plant C stoichiometric traits.

Data analysis

We ran all the analyses in R, version 4.4.2 (R Core Team 2024). For **H1**, we performed a Principal Component Analysis (PCA; scaled data) on the eleven C-allocation traits as a preliminary step to observe whether and how traits co-vary, plotting the occupancy of the three focal species, using the *factoextra* package (Kassambara and Mundt 2020). We assessed differences between species occupancy in the multivariate functional space via a PERMANOVA test (dissimilarity index based on Gower's distance, with 9999 permutations), using the *vegan* package (Oksanen et al. 2024). Then, we quantified pairwise trait co-variation across the eleven C-allocation traits, using the *corrplot* package (Wei and Simko 2024). However, given the importance of multidimensional trait co-variation (Carta et al. 2025) and to account for possible autocorrelation in the data due to structuring factors (making our data non-independent), we also modelled the multivariate co-variation of such traits while considering the effect of five random factors (abiotic variables: site, Nfires; biotic variables: species identity, Nforks, Nstems) within the Bayesian framework offered by Hierarchical Modelling of Species Communities (Warton et al. 2015), using the *Hmsc* package (Tikhonov et al. 2020). Additionally, we executed a variance partitioning analysis to estimate the relative role of the five random factors on the multivariate expression of the C-allocation traits. We implemented the Hierarchical Modelling of Species Communities framework to address also the other two hypotheses. For **H2**, we set leaf $\delta^{13}C$ as the predictor of $\delta^{13}C$ in the stem, belowground coarse organ and soil – because C isotopic discrimination occurs primarily during leaf photosynthesis. In this case we dealt with each species separately, considering the effect of the other random factors (site, Nfires, Nforks [for *E. arborea* and *Q. ilex*] or Nstems [for *C. salviifolius*]) on the observed trait relationships. For **H3**, we selected three easy-to-collect aboveground traits (basal stem diameter, SDMC, LDMC) – that previous research reported be linked to (e.g. LDMC; Fortunel et al. 2009; Pakeman et al. 2011), or it is meaningful to link to ecosystem functioning – setting them as predictors of two selected key ecosystem functions (soilC and soilCN) treated as response variables. In this case as well we worked with each species separately, accounting for the effect of the other random factors (site, Nfires, Nforks [for *E. arborea* and *Q. ilex*] or Nstems [for *C. salviifolius*]) on the observed relationships. In all Bayesian models devised to tackle **H1-H3**, we worked on log-transformed trait-data and ran four independent chains of 130,000 iterations each over four MCMC chains with the first 30,000 iterations discarded as burn-in and a thinning interval of 100, resulting in 10,000 posterior samples. We assessed the posterior distribution and relationship robustness based on visual inspection of Gelman's diagnostics and on support level threshold > 0.95.

Results

The first PCA dimension is mainly formed by the coordination of $\delta^{13}C$ of different organs, whereas along the second dimension we observe a trade-off between aboveground growth (basal stem diameter, canopy diameter) vs %C allocated to stems and to belowground coarse organs (Fig. 1). The three focal

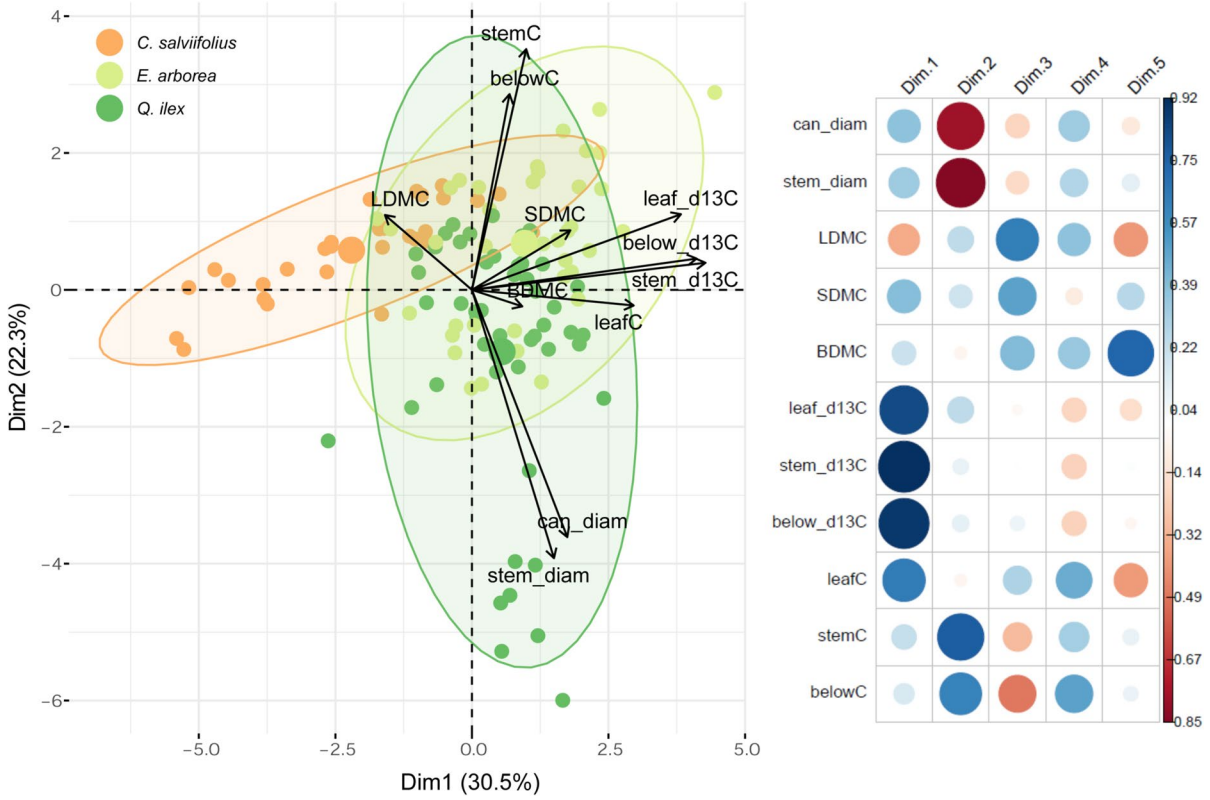


Fig. 1 PCA biplot of the eleven C-allocation traits showing the occupancy in the multivariate functional space of the three focal Mediterranean woody species (left) and trait loadings on the main dimensions (right; for variance explained by main dimensions, see Fig. S1); can_diam = canopy diameter of the entire individual, stem_diam = basal stem diameter

Mediterranean woody species separate along the first axis, namely individuals of *C. salviifolius* are consistently characterized by organs with lower carbon concentration (%C) and $\delta^{13}C$ values than individuals of *E. arborea* and *Q. ilex*. The PERMANOVA test confirms that species differ significantly in their occupancy in multivariate functional space (Full model: $R^2 = 0.36$***; *C. salviifolius* vs *E. arborea*: $R^2 = 0.34$***; *C. salviifolius* vs *Q. ilex*: $R^2 = 0.38$***; *E. arborea* vs *Q. ilex*: $R^2 = 0.23$***; see Table S1 for model summary statistics).

Correlation analysis shows that DMC of different organs (leaf, stem, belowground coarse organ) is completely decoupled from %C (and almost entirely from $\delta^{13}C$) of the relative organ – regardless of taking or not the effect of random factors into account (Fig. 2), which aligns with the patterns observed in the PCA related to trait loadings along the main dimension of functional variation (Fig. 1). In the models taking into account the structuring effects of different biotic and abiotic factors on pairwise trait correlation, we find that the random factors "site" and "species" do not change most of the observed patterns compared to the trait correlation ran without including any random factor (Fig. 2). We reveal instead how the random factors associated with disturbance regime ("Nfires") and individual developmental stage ("Nforks", "Nstems") exert a stronger effect on trait correlation, with several pairwise trait co-variation disappearing (Fig. 2).

The variance partitioning showing the relative effect of the five random factors on the expression of each C-allocation trait (Fig. 3) indicates how: 1) species identity is particularly relevant for %C and $\delta^{13}C$ of different plant organs, 2) ontogeny affects mostly size-related traits and BDMC, 3) fire regime influences mainly LDMC and SDMC, and 4) the structuring effect of site tends to remain constant across all traits.

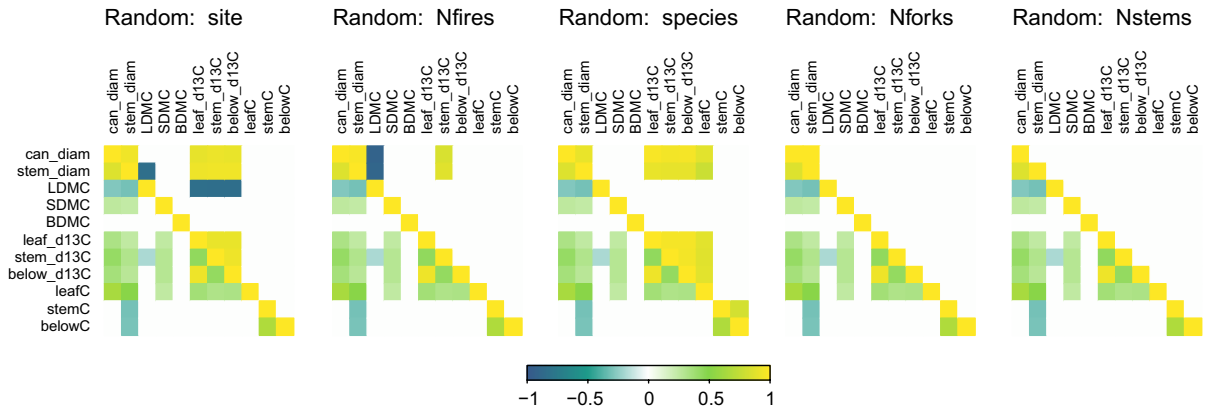


Fig. 2 Correlation matrices showing the pairwise trait correlation without considering any effect of potentially structuring factors (*lower diagonal*) and once the effect of each abiotic (site, Nfires) and biotic (species identity, ontogeny [Nforks, Nstems]) random factor is accounted for (*upper diagonal*); can_diam = canopy diameter of the entire individual, stem_diam = basal stem diameter. Model diagnostics and summary statistics are reported in Fig. S2

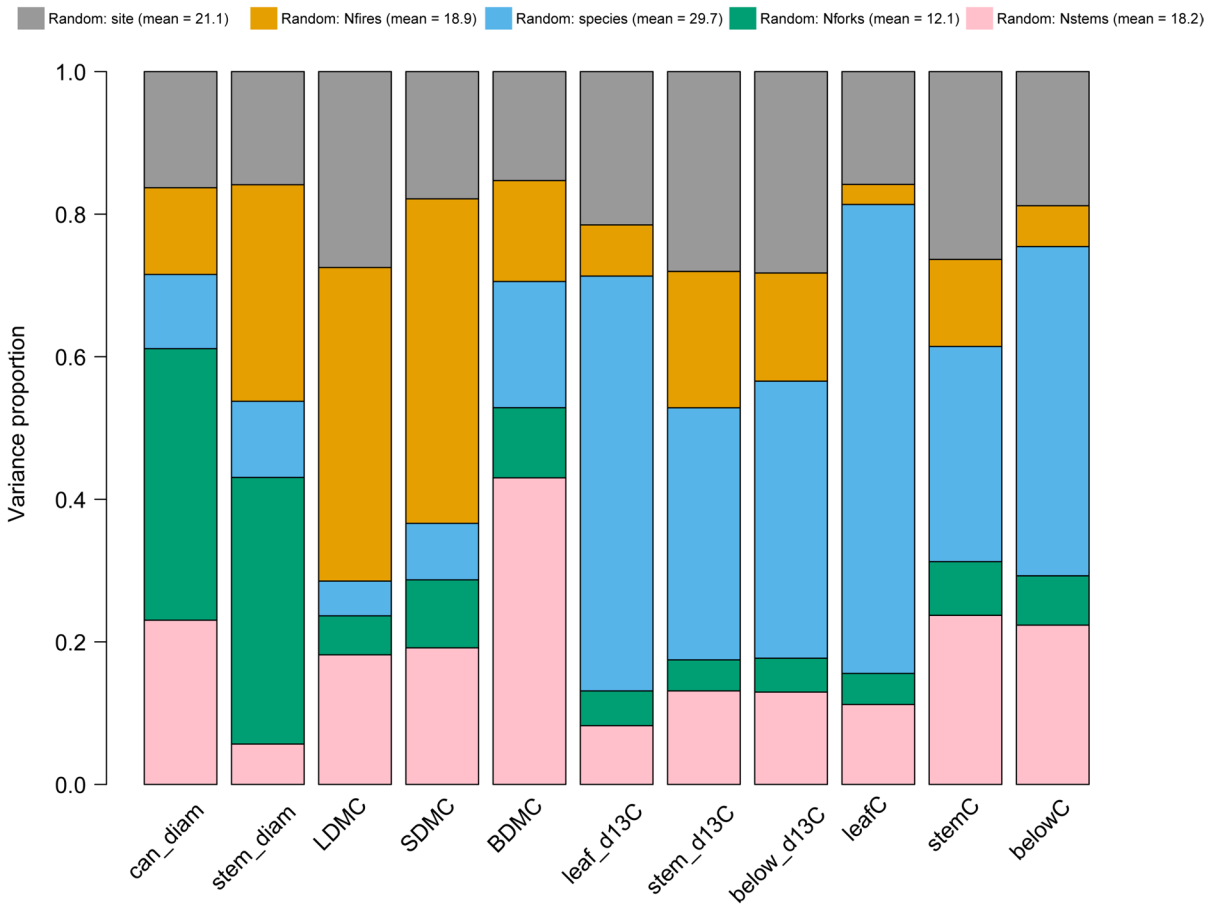


Fig. 3 Variance partitioning quantifying the relative role of random factors in shaping the expression of each C-allocation trait; can_diam = canopy diameter of the entire individual, stem_diam = basal stem diameter

We find that $\delta^{13}C$ can be effectively traced across different plant organs, and this evidence emerges for each of the three focal Mediterranean woody species (Fig. 4). The occurrence of a plant-soil continuum of C instead is not supported, namely the leaf $\delta^{13}C$ has no predictive ability for upper-soil $\delta^{13}C$ (Fig. 4).

The selected plant functional traits (basal stem diameter, SDMC, LDMC) prove unable to consistently predict the two selected soil ecosystem functions, i.e. soilC and soilCN. Only LDMC for *Q.ilex* is negatively associated with soilC (posterior mean [±95% quantile] = −2.728861 [−5.1701, −0.27738]) and basal stem diameter shows a marginal positive link to soilC for *E. arborea* (posterior mean [±95% quantile] = 0.5821 [−0.09268, 1.2277]; all model diagnostics and summary statistics are reported in Fig. S4).

Discussion

Although limited to three woody species and three sites, our study contributes to advancing the basic biological understanding of plant life in the fire-prone Mediterranean Basin, given the phylogenetic and functional variation represented by the selected woody species. We illustrate how 1) plants can form integrated functional strategies for C allocation while challenging widely assumed yet poorly tested links, such as the observed functional decoupling between organ's DMC and %C or $\delta^{13}C$, and 2) often neglected biological features (i.e. ontogeny) as well as disturbance regime (e.g. fire) can largely affect trait coordination.

C-allocation traits co-vary forming coordinated functional strategies, yet dry matter content of different organs is decoupled

We identify fundamental axes of variation forming coordinated C-allocation strategies, with the focal Mediterranean woody species exhibiting distinct occupancy in the multivariate functional space, indicative of distinct C-related functional niches (Fig. 1). This pattern might be linked to the focal species belonging to different plant functional types and growth forms: *C. salviifolius* is a broadleaved sclerophyllous reseeder small shrub, *E. arborea* is a needle-like non-sclerophyllous resprouter shrub, *Q. ilex* is a broadleaved sclerophyllous resprouter shrub or tree. The first dimension of functional variation indicates a tight whole-plant trait coordination for $\delta^{13}C$ of different organs, such that the C absorbed in the leaves can be traced across various

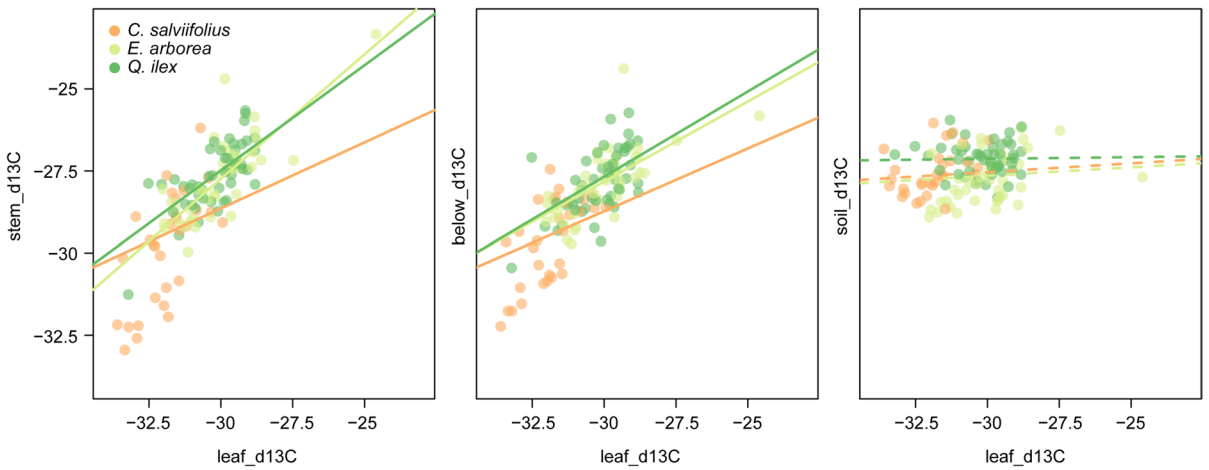


Fig. 4 Scatterplots displaying the relationships of $\delta^{13}C$ between different plant organs and the upper soil layer in the three focal woody species (*C. salviifolius*, *E. arborea*, *Q. ilex*). We set leaf $\delta^{13}C$ as predictor of $\delta^{13}C$ in the stem (left), belowground coarse organ (center) and soil (right). Solid lines indicate regression models with support level > 0.95, whereas dashed lines indicate support level < 0.95. This result takes into account the data-structuring effect associated with study site, Nfires, ontogeny (Nstems for *C. salviifolius*; Nforks for *E. arborea* and *Q. ilex*). Model diagnostics and summary statistics are reported in Fig. S3

plant organs – as further corroborated by other findings (Fig. 2 and 4). Species-wise, *C. salviifolius* exhibits consistently more negative values of leaf, stem and belowground coarse organ $\delta^{13}C$, compared to *E. arborea* and *Q. ilex*, suggesting lower demand to limit evapotranspiration in the small shrub *C. salviifolius* (mitigated by leaf shedding; Grant et al. 2014) compared to the other two larger woody species during warm and dry Summers (Muñoz-Gálvez et al. 2025). The second dimension depicts an aboveground growth-C storage functional trade-off, implying that C stored in stems, thick roots or lignotubers may boost aboveground (re)growth of the three Mediterranean woody species (Blumstein et al. 2022).

When the effect of biotic and abiotic random factors is accounted for in trait co-variation, we could appreciate the structuring effects of fire and ontogeny (Fig. 2). This suggests that different fire regime conditions and different developmental stages of sampled individuals are characterized by distinct trait correlations and potentially different growth forms (Laurans et al. 2024; Chiminazzo et al. 2026) – as also observed for size-related traits in a savanna woody species experiencing different disturbance regimes (Millan et al. 2024). Conversely, sampling site and species identity played a secondary role in driving the variability in our data. This would suggest that micro- and macro-environmental conditions defining the three study sites (also corroborated by the similar amount of variability explained by this factor across traits in the variance partitioning; Fig. 3) as well as evolutionary history (considering that the three species belong to phylogenetically distant plant families) may operate as secondary factors in shaping C-allocation strategies considered in our study. Additionally, the evidence for aboveground growth-traits largely shaped by ontogeny while DMC of leaves and stems strongly affected by fire regime aligns with research stemming from open ecosystems in other fire-prone regions (e.g. tropical savannas; Chiminazzo et al. 2026). These patterns suggest that larger plants tend to be more advanced in their development and that denser and more water conservative organs can be promoted by a fire regime that favors open, hence drier and warmer environments (Pellegrini et al. 2023; Alam et al. 2025), potentially creating a positive feedback loop for fire occurrence (Baudena et al. 2020; Magnani et al. 2023; Ottaviani et al. 2026a). This information can be used to refine management actions devised to promote ecosystem resilience.

All our analyses demonstrate that denser tissues of different plant organs are decoupled from the C concentration and isotopic composition of the relative organ in the focal Mediterranean woody species. This result challenges the prevailing C economics view in trait-based plant ecology (e.g. Givnish 1986; Westoby et al. 2002; Wright et al. 2002; Reich et al. 2003). Several biological and functional reasons could be behind this lack of co-variation. First, in open ecosystems carbon may not be a limiting factor for key plant functions (such as growth, survival, reproduction) because light is abundant. Second, variation in DMC of different organs may be better linked to within-organ water availability and regulation, not necessarily to proportionally more carbon allocated to the organ. In other words, the assumption that denser and longer-lived leaves (resource-conservative) are proportionally more "expensive" to plants in terms of C investments than less dense and shorter-lived "cheaper" leaves (resource-exploitative) is not supported in our analysis. At the same time, the expected functional relationship between LDMC and leaf $\delta^{13}C$ (e.g. Bernard-Verdier et al. 2012; Ottaviani and Keppel 2018) does not occur in our data, suggesting that denser and more water-conservative leaves are not tightly associated with enhanced water-use efficiency but possibly to within-organ water content regulation. Our results indicate that Mediterranean woody species may respond to aridity by exhibiting different coordinated leaf strategies, pointing to structural adjustments that support internal water balance (Coskun et al. 2016; Alon et al. 2024). However, this inference requires further investigation, extending to a larger species pool and other mediterranean-type ecosystems, ideally through experimental manipulation of water and light availability as well as temperature, examining to what extent leaf physiological ($\delta^{13}C$) vs morphological (LDMC) adjustments are (de)coupled.

No evidence for the occurrence of a $\delta^{13}C$ plant-soil continuum

The analysis devised to test whether a plant-soil continuum for C occurs (through tracing $\delta^{13}C$ in the plant and soil) does not detect evidence supporting this hypothesis under our sampling design. The decoupling between plant and soil $\delta^{13}C$ emerged

consistently across the three species, indicating that plant tissues and soil may behave as distinct compartments for C dynamics in our study. However, other mediating, and unaccounted for factors related to soil conditions or root traits affecting biogeochemical cycles – such as soil pH and humidity, microbiome diversity, presence of charcoal, mineral composition, rate of heterotrophic respiration, plant rooting depth (De Deyn et al. 2008; Metcalfe et al. 2011; Bardgett et al. 2014; February et al. 2020) – could contribute to explain this lack of relationship. We acknowledge that our soil sampling was restricted to the uppermost layer (~5 cm deep). While this layer is largely affected by litter decomposition and includes belowground coarse organs such as thick roots or lignotubers (Ottaviani et al. 2024), fine roots and most active rhizosphere processes can occur deeper in the soil – particularly under water-scarcity conditions. Consequently, our shallow soil sampling may have reduced our ability to capture C potentially translocated from the plant to the soil via fine root exudates or biological associations (e.g. mycorrhizas), thereby contributing to the lack of $\delta^{13}C$ correlation observed between plant organs and soil. Still, most of our study areas were characterized by shallow soils (5–10 cm deep; personal field observation) so we expected the soil sampling could include a considerable amount of fine roots. Nonetheless, future studies sampling across multiple soil depth increments and explicitly targeting rhizosphere-associated pools are needed to more comprehensively assess whether plant assimilation isotopic signatures propagate into soil carbon across depth layers and turnover times.

Our findings further support the existence of a tight whole-plant coordination for $\delta^{13}C$, namely across different plant organs – a pattern that consistently emerges across the three focal Mediterranean woody species. Leaf $\delta^{13}C$, reflects photosynthetic discrimination during CO_2 fixation under specific environmental and physiological conditions (Farquhar et al. 1989; Hultine and Marshall 2000; Cernusak et al. 2013). This C is then translocated through phloem to heterotrophic tissues where it is incorporated into structural and storage compounds in stems and belowground organs. Our analysis detects how the two woody reprouters *E. arborea* and *Q. ilex* tend to have a similar model slope and intercept compared to the reseeder *C. salviifolius* (Fig. 4), suggesting that species belonging to different life histories are characterized by different C-allocation strategies. For example, resprouting grasses tend to be more resource-conservative than reseeder grasses (Simpson et al. 2021), which may then affect the speed of biomass recovery after disturbance, thus allocation of C and other resources. Yet, post-fire responses can largely vary across different growth forms, such as between grasses and woodies (Simpson et al. 2021), so this interesting comparative topic in plant functional and disturbance ecology would deserve further scrutiny. Taken together, our results indicate that fire regime can be an important factor shaping plant C-related functional strategies in the focal Mediterranean woody species, as also highlighted by correlation analysis.

Selected easy-to-collect plant traits cannot predict C stock and nutrient status of upper soil layers

LDMC is an easy-to-collect and widely used plant functional trait. This is because LDMC has shown its ability, at different scales and in various biogeographic contexts, to i) capture water-related strategies, ii) estimate plant responses to environmental variation, iii) mediate impacts of these changes on key ecosystem functions, such as litter decomposability and therefore soil nutrient and carbon cycling (Garnier et al. 2004; Kazakou et al. 2006; Fortunel et al. 2009; Hodgson et al. 2011; Pakeman et al. 2011). However, in our dataset LDMC as well as the other two selected traits (basal stem diameter, SDMC) proved their almost complete inability to predict two key soil ecosystem functions (soilC, soilCN). LDMC could predict soilC only for *Q. ilex*, suggesting that for this evergreen broadleaved sclerophyllous species, leaf shedding and resulting litter formation and decomposition can affect soil C pool. However, this pattern does not emerge for the other two species – together with the weak positive link between basal stem diameter and soilC for *E. arborea* and complete decoupling between traits and soilCN – and indicates the inconsistent predictive power of these traits to estimate C stock and nutrient status of upper soil layers, which aligns with the lack of detection for a plant-soil continuum for $\delta^{13}C$. A possible explanation for this plant and soil decoupling could refer to a scaling mismatch between individual-level measures (traits) and ecosystem-level measures (soil functions) – a well-known matter in trait-based plant ecology

when examining multiple organizational levels (e.g. Ackerly et al. 2002; Kichenin et al. 2013; Bardgett et al. 2014; García-Callejas et al. 2025). Plant traits, although carrying a clear biological and functional meaning, do not necessarily scale directly, linearly or additively at higher organizational levels, such that they may or may not be able to predict specific ecosystem functions. We therefore encourage further examination of possible determinants of those mismatches and how to bridge them, being a crucial task in basic and applied plant and ecosystem ecology.

Outlook

The selected widely used and easy-to-collect traits were not capable of effectively and consistently predicting C stock and nutrient status of upper soil layers in our Mediterranean case study. However, we encourage future studies not to abandon this key research line for basic and applied ecology. We suggest to sampling deeper in the soil and considering a larger sample size with more species (including an array of different life histories, life and growth forms) and sites from different regions hosting mediterreanean-type ecosystems as well as other open biomes (e.g. tropical savannas) to thoroughly test the generality of our findings. We also recommend extending to other stoichiometric traits (e.g. $\delta^{15}N$) to have a more complete view on carbon-nutrient exchanges occurring at the plant-soil interface – C flowing downwards from the leaves to stems, belowground organs and then eventually into the soil (as attempted in this study) whereas N flowing upwards, such as N acquired in the soil through the fine roots (and mycorrhizal or rhizobial associations) could be traced through stems and leaves. This piece of information can pave the way toward a more mechanistic understanding of plant-soil interactions and feedbacks.

Acknowledgements We thank Luciano Spaccino for helping with the lab-work. Ilaria Baneschi, Mara Baudena, José Maria Costa-Saura, Ettore D'Andrea assisted with fieldwork and commented on an earlier version of the manuscript. This manuscript stemmed from the activity of the transdisciplinary "Wildfires and Biodiversity" working group within the National Biodiversity Future Center (NBFC).

Author contributions Gianluigi Ottaviani conceived the original research idea, which was further developed and refined thanks to inputs from Angelino Carta, Silvia Portarena, Marta Magnani. Gianluigi Ottaviani, Marta Magnani, Mauro Lo Cascio collected plant material and scored traits in the field. Mathieu Millan assisted with trait selection. Silvia Portarena, Carlotta Volterrani, Irene Tunno carried out the lab-work related to all stoichiometric traits. Angelino Carta performed statistical analyses, with inputs from Gianluigi Ottaviani. Gianluigi Ottaviani wrote the first draft of the manuscript and led the revision process. Angelino Carta, Silvia Portarena, Marta Magnani assisted with the drafting, and all co-authors contributed to revisions of the manuscript and approved its submission.

Funding Open access funding provided by Consiglio Nazionale Delle Ricerche (CNR) within the CRUI-CARE Agreement. This research acknowledges the support of the National Biodiversity Future Center (NBFC), funded by the Italian Ministry of University and Research, P.N.R.R., Mission 4 "Education and Research" – Component 2: "From research to business", Investment 1.4, Project CN00000033 (Project funded by the European Union—NextGenerationEU). Irene Tunno is supported by the Italian Integrated Environmental Research Infrastructures System (IR0000032, ITINERIS, D.D. n. 130/2022 – CUP B53C22002150006), funded by the Italian Ministry of University and Research, P.N.R.R., Mission 4 "Education and Research" – Component 2: "From research to business", Investment 3.1: "Fund for the realization of an integrated system of research and innovation infrastructures" (Project funded by the European Union—NextGenerationEU).

Data availability The dataset used in this research is publicly available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.31150144 (Ottaviani et al. 2026b).

Declarations

AI statement No AI tools were used in this research.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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