

4 **Relationships between leaf morphological traits, nutrient**
5 **concentrations and isotopic signatures for Mediterranean**
6 **woody plant species and communities**7 **María T. Domínguez · Cristina Aponte ·**
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11 © Springer Science+Business Media B.V. 201212 **Abstract**13 *Background and aims* Soil factors are driving forces
14 that influence spatial distribution and functional traits
15 of plant species. We test whether two anchor mor-
16 phological traits—leaf mass per area (LMA) and leaf
17 dry matter content (LDMC)—are significantly relat-
18 ed to a broad range of leaf nutrient concentrations in
19 Mediterranean woody plant species. We also explore
20the main environmental filters (light availability, soil 21
moisture and soil nutrients) that determine the pat- 22
terns of these functional traits in a forest stand. 23
Methods Four morphological and 19 chemical leaf 24
traits (macronutrients and trace elements and $\delta^{13}\text{C}$ 25
and $\delta^{15}\text{N}$ signatures) were analysed in 17 woody plant 26
species. Community-weighted leaf traits were calcu- 27
lated for 57 plots within the forest. Links between 28
LMA, LDMC and other leaf traits were analysed at 29
the species and the community level using standar- 30
dised major axis (SMA) regressions 31
Results LMA and LDMC were significantly related to 32
many leaf nutrient concentrations, but only when us- 33
ing abundance-weighted values at community level. 34
Among-traits links were much weaker for the cross- 35
species analysis. Nitrogen isotopic signatures were 36
useful to understand different resource-use strategies. 37
Community-weighted LMA and LDMC were nega- 38
tively related to light availability, contrary to what was 39
expected. 40
Conclusion Community leaf traits have parallel shifts 41
along the environmental factors that determine the 42
community assembly, even though they are weakly 43
related across individual taxa. Light availability is 44
the main environmental factor determining this con- 45
vergence of the community leaf traits. 46

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Bangor, Gwynedd LL57 2UW, UK**Keywords** Community weighted means · Functional 47
traits · Leaf dry matter content · Leaf mass per 48
area · Macronutrients · Specific leaf area · Isotopes 49

50 **Introduction**

51 The evolutionary radiation of vascular plants has pro-
 52 vided a wide variety of leaf shapes and structures for a
 53 few common functions of intercepting light, fixing
 54 carbon and regulating water balance. Global patterns
 55 of leaf traits have been mostly related with climatic
 56 patterns (Wright et al. 2004a, 2005) but recent studies
 57 have remarked the importance of edaphic factors as
 58 driving forces determining plant functional traits
 59 (Holdaway et al. 2011; Lambers et al. 2010).

60 Leaf traits are related among them by causal relation-
 61 ships that limit their possible combinations and impose
 62 their covariation with the result of trade-offs among
 63 functionally distinct traits (Cornelissen et al. 1999;
 64 Meziane and Shipley 2001; Shipley et al. 2006).
 65 Among leaf traits, the leaf mass per area (LMA)—or
 66 its inversed value, specific leaf area (SLA)—has been
 67 frequently used as an indicator of differential functional
 68 strategies in plant species (Coley 1988; Cornelissen et
 69 al. 1999; Reich et al. 1991, 1998; Wright et al. 2004a).
 70 Two opposite functional strategies can be distinguished
 71 from the range of trait variation that defines the *leaf*
 72 *economics spectrum* (Diaz et al. 2004; Wright et al.
 73 2004). At one extreme, stand species with a conserva-
 74 tive resource-use strategy usually showing high values
 75 of LMA, high-density tissues, low leaf-N concentration
 76 and long leaf-life span (Coley 1988; Reich et al. 1991,
 77 1998; Villar et al. 2006), that allow them to increase
 78 competitive abilities in dry and nutrient-poor environ-
 79 ments (Aerts 1995; Hobbie 1992). In contrast, species
 80 with a predominant resource-acquisition strategy have
 81 opposite attributes commonly associated to rapid re-
 82 source capture and high relative growth rate (Diaz et
 83 al. 2004; Poorter and Garnier 1999; Ruíz-Robledo and
 84 Villar 2005; Wright and Westoby 2001), that allow them
 85 to be more dominant in moist and fertile areas (Grime et
 86 al. 1997; Reich et al. 1999).

87 Cross-species analyses at global-scale have demon-
 88 strated that LMA, N and P leaf concentrations, and
 89 photosynthetic capacity are strongly inter-correlated
 90 (Poorter et al. 2009; Wright et al. 2004a). However,
 91 multivariate analyses of leaf composition have shown
 92 that the N and P variation trend (so-called nucleic acid-
 93 protein set of elements) differs from the trend for other
 94 elements such as Ca, K and Mg, which have predomi-
 95 nant structural and enzymatic functions (Aponte et al.
 96 2011; Garten 1978; Watanabe et al. 2007). The differ-
 97 ences among species in nutrient requirements, not only

of N and P, but also of Ca, K, Mg and micronutrients 98
 such as Mo, Fe and Cu, may favour their coexistence by 99
 separation of their biogeochemical niches (sensu 100
 Peñuelas et al. 2008, 2011). 101

Although most studies have used LMA as the anchor 102
 trait (sensu Ackerly 2004), leaf dry matter content 103
 (LDMC, dry leaf mass per water-saturated fresh leaf 104
 mass) has proved to be equally or more important trait. 105
 LDMC is linked to the leaf protein concentration and 106
 cytoplasmic volume, and therefore to plant metabolism 107
 (Wilson et al. 1999). It can determine the aboveground 108
 primary productivity and the digestibility of the leaf 109
 (Pontes et al. 2007), the decomposability of the litter 110
 (Garnier et al. 2004), and sometimes it can be better 111
 correlated with soil fertility than LMA (Hodgson et al. 112
 2011; Rusch et al. 2009). However, very few works 113
 have analysed the relationships between LDMC and a 114
 broad range of leaf nutrient concentrations. 115

Isotopic signatures (expressed as N and C isotope 116
 ratios) also provide useful information to characterize 117
 different strategies of resource acquisition in plants. The 118
 leaf N isotopic signature integrates different factors 119
 involved in N acquisition, such as the source and the 120
 soil depth from which N is taken up, the association with 121
 mycorrhizal and symbiotic microorganisms, and the 122
 within-plant processes of N transport and assimilation 123
 (Högberg 1997). The type of mycorrhizal interaction 124
 largely explains the differences in $\delta^{15}\text{N}$ among plants 125
 at a global scale (Craine et al. 2009), as well as among 126
 coexisting species at the community scale (Hobbie et al. 127
 2000). Ericoid and ectomycorrhizal strategies, which are 128
 usually related to low leaf $\delta^{15}\text{N}$ values (Craine et al. 129
 2009; Kranabetter and MacKenzie 2010), are linked to 130
 resource-conservation attributes, such as low plant 131
 growth rates, low foliar nutrient concentrations and poor 132
 litter decomposability (Cornelissen et al. 2001; Meers et 133
 al. 2010). Negative $\delta^{15}\text{N}$ values in leaves may be indic- 134
 ative of a high dependence on mycorrhizal interactions 135
 for N uptake, which is increased under low soil N 136
 availability (Hobbie et al. 1999, 2000). The linkages 137
 between leaf $\delta^{15}\text{N}$ values and other leaf traits remain 138
 largely untested. In contrast, the well-known relation- 139
 ship between $\delta^{13}\text{C}$ and water use efficiency (Farquhar et 140
 al. 1989) has promoted the frequent use of this isotopic 141
 signature to detect functional trait syndromes (e.g., 142
 Escudero et al. 2008; Lamont et al. 2002). 143

Most studies on leaf traits have been carried out at 144
 the species level (by comparing simple averages of 145
 traits by species). To scale up from the species to the 146

147 community level, recent studies have incorporated the
 148 use of community-weighted-means (Díaz et al. 2007;
 149 Violle et al. 2007), where functional traits are weight-
 150 ed by the relative abundance of each of the dominant
 151 constituting species. These community-aggregated
 152 values are particularly helpful to study the response
 153 of traits to environmental factors, and to explore the
 154 links between traits and ecosystem processes and serv-
 155 ices (Garnier et al. 2004). The environmental factors
 156 determine how species replace each other, and thus,
 157 how different the weighted averages are across the
 158 studied plots. A close link between traits at the com-
 159 munity level would suggest that the environmental
 160 filters that determine such community assembly pro-
 161 mote the convergence of certain individual traits in
 162 that community. Since dominant species tend to have
 163 leaf trait values better linked to their environments
 164 than less abundant species, we expect to find stronger
 165 associations among traits and clearer response of traits
 166 to environmental factors when using the abundance-
 167 weighted approach, rather than when using the aver-
 168 age trait value for the species pool in the community
 169 (Ackerly et al. 2002; Cingolani et al. 2005, 2007).

170 In this study we explored the spectrum of leaf traits
 171 (mainly LMA and LDMC) and their relationships with
 172 nutrient concentrations and isotopic signatures in a
 173 Mediterranean woodland, testing these relationships
 174 at both the species and the community level. We
 175 pursued two particular objectives: first, we analysed
 176 the relationships between LMA, LDMC and several
 177 nutritional traits: leaf concentrations of macro- and
 178 micronutrients, non-essential trace elements, and C
 179 and N isotopes. Our hypothesis was that species with
 180 a marked resource-acquisition strategy (i.e., with low
 181 values of LMA) will exhibit: i) higher nutrient leaf
 182 concentrations, especially for those nutrients with a
 183 prevalent photosynthetic function; ii) a lower depen-
 184 dence on mycorrhizal interactions for N-uptake (i.e.,
 185 higher leaf ¹⁵N values); and iii) a reduced water-use
 186 efficiency (i.e., lower ¹³C values). We tested whether
 187 the links among traits at the species level (which
 188 would reflect the evolutionary covariation of traits in
 189 a species pool) are similar to those links at the com-
 190 munity level (which would reflect the convergence of
 191 traits promoted by the environmental filters).

192 Second, we studied the changes in community
 193 weighted and unweighted means of LMA, LDMC
 194 and nutrient-related leaf traits along a broad and het-
 195 erogeneous range of environmental conditions in order

196 to identify the main abiotic factors structuring those
 197 patterns (light, soil water and soil fertility). The general
 198 hypothesis here was that the dominance of the species in
 199 the community is more strongly filtered by the abiotic
 200 factors than the presence/absence of individual taxa in a
 201 species pool. Thus the abundance-weighted traits are
 202 expected to show higher relationships with the environ-
 203 mental factors than the unweighted (based on presence/
 204 absence) traits. In particular, the community-weighted
 205 LMA and LDMC values are expected to decrease with
 206 increasing forest canopy density (lower light) as well as
 207 with increasing nutrient and water availability in soil,
 208 due to a higher proportion of species with a predominant
 209 resource-acquisition strategy.

Material and methods

Study area, species selection and sampling design

210
 211
 212 The study area is located in the Aljibe Mountains, a
 213 protected mixed oak forest area in southern Spain. The
 214 climate is of a sub-humid Mediterranean type with mild,
 215 wet winters alternating with hot, dry summers and most
 216 rainfall (95 %) occurring from October to May. The
 217 bedrock is dominated by Oligo-Miocene sandstone
 218 and produces acidic, nutrient-poor soils, which are fre-
 219 quently interspersed with layers of marl sediments,
 220 yielding soils richer in clay (*Haploxererts*, Soil Survey
 221 Staff 2006). The vegetation is dominated by the ever-
 222 green cork oak (*Q. suber* L.) mixed with the winter-
 223 deciduous Algerian oak (*Q. canariensis* Willd.), which
 224 is locally abundant in the valley bottoms (Urbietta et al.
 225 2008). The study was conducted in a forest stand (La
 226 Saucedá; 36° 31' 54"N, 5° 34' 29" W) located at an
 227 altitude of 530–560 m on a NW facing slope. The mean
 228 annual temperature is 15.5 °C, and the mean annual
 229 rainfall is 1470 mm. Tree density in the stand is rela-
 230 tively low, with 219 stems ha⁻¹ and a basal area of
 231 22 m² ha⁻¹ (see more details about the forest site in
 232 Pérez-Ramos et al. 2008 and Quilchano et al. 2008).

233 To represent the dominant vegetation of the studied
 234 mixed-oak forest, we selected seventeen woody plant
 235 species, including the dominant oak tree species (*Q.*
 236 *suber* and *Q. canariensis*) and the most abundant
 237 shrubs and vines in the understorey (Table 1). They
 238 were also selected to cover the widest variability of
 239 leaf traits in the area. Nomenclature follows Valdés et
 240 al. (1987), with exception of *Teline linifolia* (Talavera

Table 1 List of the 17 woody plant species selected for trait measurements. The family, life habit, leaf habit and nutritional strategies are indicated. The mean abundance (in a 100 %-scale) and frequency (presence in % of plots) for each species were estimated in the 57 plots where community approach was applied (na, not available because of low frequency)

Species	Code	Family	Life habit	Leaf habit	Nutritional strategy ^a	Abundance mean (%)	Frequency (%)
<i>Crataegus monogyna</i> Jacq	Cm	Rosaceae	Arb-Shrub	Winter deciduous	ECT	4.0	3.5
<i>Cistus salvifolius</i> L.	Cs	Cistaceae	Shrub	Evergreen	ECT	11.5	3.5
<i>Calicotome villosa</i> (Poir.) Link	Cv	Fabaceae	Shrub	Summer deciduous	N-FIX	63.9	14.0
<i>Erica arborea</i> L.	Ea	Ericaceae	Arb-Shrub	Evergreen	ERI	28.2	22.8
<i>Erica scoparia</i> L.	Es	Ericaceae	Shrub	Evergreen	ERI	29.4	14.0
<i>Lonicera implexa</i> Aiton	Li	Caprifoliaceae	Vine	Evergreen	ARB	11.1	1.8
<i>Osyris alba</i> L.	Oa	Santalaceae	Shrub	Evergreen	HPAR	na	<1
<i>Phillyrea latifolia</i> L.	Phyl	Oleaceae	Arb-Shrub	Evergreen	ARB	5.4	33.3
<i>Pistacia lentiscus</i> L.	Plen	Anacardiaceae	Arb-Shrub	Evergreen	ARB	20.8	45.6
<i>Phlomis purpurea</i> L.	Pp	Labiatae	Shrub	Evergreen	ARB	14.2	29.8
<i>Quercus canariensis</i> Willd	Qc	Fagaceae	Tree	Winter deciduous	ECT	15.7	26.3
<i>Quercus suber</i> L.	Qs	Fagaceae	Tree	Evergreen	ECT	26.3	43.9
<i>Rosa pouzini</i> Tratt.	Ros	Rosaceae	Shrub	Winter deciduous	ARB	na	<1
<i>Rubus ulmifolius</i> Schott	Ru	Rosaceae	ShrubVine	Evergreen	ARB	2.4	12.3
<i>Smilax aspera</i> L.	Sa	Smilacaceae	Vine	Evergreen	ARB	16.6	38.6
<i>Teucrium fruticans</i> L.	Tf	Labiatae	Shrub	Evergreen	ARB	14.1	12.3
<i>Teline linifolia</i> (L.) Webb in Webb and Berthel.	Tl	Fabaceae	Shrub	Evergreen	N-FIX	13.3	14.0

Arb-Shrub arborescent shrub; *ARB* arbuscular-mycorrhizal species; *ECT* ectomycorrhizal species; *ERI* ericoidal-mycorrhizal species; *HPAR* hemiparasitic species; *N-FIX* nitrogen-fixing species

^a Mycorrhizal types according to Marenmani et al. (2003)

and Gibbs 1999). In late spring 2008, during the peak of vegetative growth, 32 plots (3×3 m) were set up within the forest site covering a wide range of environmental conditions. In each plot, one healthy adult of each of the most dominant woody plant species was collected for leaf trait measurements, making a total of 85 individuals (five per species) distributed among the 32 plots. For each selected individual, we collected at least two branches with young, fully expanded leaves from those parts of the plant with the highest light exposition. The branches were placed in plastic bags and transported in a chilled, dark container to the laboratory, where the plants were stored in darkness at 15 °C with the stem bases submerged in water for at least 12 h to fully rehydrate the leaves.

Each of these 32 plots was characterised by analysing soil samples (0–25 cm depth) for physical and chemical properties. Soil texture was determined by the Bouyoucos hydrometer method; pH was measured in a 1:2.5 soil: water suspension; soil organic matter was determined by

combustion at 450 °C and total N was determined by Kjeldahl digestion. Available P was estimated by the Bray method; Ca, K and Mg were extracted with 1 M ammonium acetate and determined by atomic absorption spectrophotometry. The availability of micronutrients (Cu, Fe, Mn and Zn) and S was determined using an EDTA solution and analysed by ICP-OES (inductively coupled plasma optical emission spectrophotometry; Thermo Jarrell Ash Corporation, Franklin, Massachusetts, USA). See details on methods for soil analyses in Sparks (1996) and a data summary in Table S1.

Leaf trait measurements

Morphological traits All leaf measurements were conducted following the criteria defined by Cornelissen et al. (2003). Five rehydrated and fully expanded young leaves per individual were harvested and weighed to obtain the lamina and petiole fresh mass. Leaf thickness (average of three measurements per leaf) was measured

with a micrometer (Electronic Digital Micrometer Comecta SA, Barcelona, Spain). For five of the 17 selected species (*C. villosa*, *E. arborea*, *E. scoparia*, *O. alba* and *T. linifolia*), leaf thickness could not be measured because of their small leaf size. Fresh leaves were scanned, and leaf area was determined by digital analysis of the images using specific software (Image-Pro Plus 4.5, Media Cybernetic Inc. USA). Finally, the leaves were oven-dried at 70 °C for 48 h and then weighed to the nearest 0.0001 g.

The leaf mass per area (LMA, g m^{-2}) was calculated as the ratio between the dry mass of the lamina and its area. Likewise, the leaf dry matter content (LDMC, g g^{-1}) was calculated as the ratio between the dry and the fresh (saturated) weights of the lamina.

Chemical traits Additional leaves were collected from each individual (from the outer part of the crown) for chemical analysis. The laminas of the leaves were separated, oven-dried (at 70 °C for 48 h) and ground using a stainless steel mill. The leaf carbon concentration was determined in an elemental analyser (CHNS Eurovector EA-3000). Nitrogen was analysed by Kjeldahl digestion (Jones and Case, 1990). The remaining macronutrients (Ca, K, Mg, P, and S), micronutrients (Cu, Co, Fe, Mn, Ni and Zn) and non-essential trace elements (Ba, Cd, Pb) were extracted by wet oxidation with concentrated HNO_3 under pressure in a microwave digester. Macronutrients (except N) were analysed by ICP-OES. Micronutrients and trace elements were analysed by inductively coupled plasma mass spectroscopy (ICP-MS; Perkin Elmer, Sciex-Elan 5000, Cambridgeshire, UK) using the methods proposed by Jones and Case (1990). Several plant reference materials were analysed to assess the quality of the analysis: NCS DC 73350 (white poplar leaves, China National Analysis Centre for Iron and Steel) and BCR-62 (olive tree leaves, European Community Bureau of Reference). Isotopic analyses of C and N in the samples were performed using a continuous flow elemental analyzer-isotopic ratio mass spectrometer (EA Thermo 1112-IRMS Thermo Delta V Advantage). The precision for both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses was approximately 0.2 per mil.

Community-level leaf traits and environmental heterogeneity

To study the variation in leaf functional traits at the community level, we calculated community-weighted

means traits. For this purpose, we selected 57 plots (3×3 m) within the same forest site, which included most of the 32 plots where the plant species were collected for leaf trait measurements (see above). The environmental conditions of each of these 57 plots was previously characterised in a parallel study focused on seedling growth (Pérez-Ramos et al. 2010). Canopy density was quantified by hemispherical photography and image analysis (Hemiview canopy analysis software ver. 2.1) and represented by the total leaf area index (LAI) and the level of light intercepted by the canopy (estimated as the global site factor, GSF). Photographs were taken at 0.5 m from the ground, using a horizontally-levelled digital camera and aimed at the zenith, using a fish-eye lens of 180° field of view. Soil volumetric water content (12 cm depth) was measured using a time-domain reflectometer (TDR, Campbell Scientific Inc., Logan, UT, USA) at every season during a year. Soil samples were taken for each plot at a depth of 0–25 cm and were analysed for macronutrients and micronutrients (see methods above).

The site spanned a high environmental heterogeneity, for example in light availability LAI ranged from 0.4 to 3 and GSF from 8 to 89 % (Table 2). Soil moisture during the growing season was dependent on soil texture, and ranged from clay-rich waterlogged soils to well-drained sandy soils with <25 % of soil moisture. Soil phosphorus availability ranged from 0.2 to 8.9 mg kg^{-1} .

The relative abundance of the woody plant species was visually estimated, by agreement between two experienced observers, as the percentage of plant cover in each 3×3 m plot. Separate 5 %-increment cover estimates were given for each species in the shrub (up to 3–4 m height), liana and tree layers. The relative abundance for each species was then calculated by dividing its specific cover estimate by the (all-layers pooled) total woody cover. Although the cover of herbaceous species also accounted for the total plant cover measure in each plot (representing, on average, a 30 % all the total plant cover), in this work we focused only on woody plants, and thus we rescaled the woody plant cover to 100 %. A total of 21 woody species were found across the 57 sampling sites, including the 17 species in our data set. Those four species not included in our data set can be considered as rare species, as they were, on average, only present in 4 out of the 57 plots.

Community-weighted-means (CWM) were calculated for every leaf trait as $\sum P_i \times \text{Trait}_i$ where P_i is

t2.1 **Table 2** Environmental variables of the 57 forest plots where community trait analysis was applied, and results of the principal component analysis (PCA). Data from Pérez-Ramos et al. (2010). GSF, global site factor

t2.2	Environmental variable	Mean ± SD	Range	PCA factors		
				Factor 1	Factor 2	Factor 3
t2.4	Leaf area index (LAI)	1.70±0.70	[0.38–3.0]	–	–	–
t2.5	Light availability (GSF)	31.7±23.7	[8.0–88.9]	–0.32	0.53	–0.68
t2.6	Soil volumetric water content (%)					
t2.7	Summer	9.3±2.8	[5.0–17.5]	–0.71	–0.20	0.17
t2.8	Spring	53.7±22.5	[25.2–>65]	–0.89	0.14	–0.04
t2.9	Soil pH	6.2±0.6	[5.4–8.3]	–0.77	–0.09	0.11
t2.10	Soil organic matter (%)	10.5±3.7	[4.8–20.6]	–0.32	–0.86	–0.06
t2.11	Soil total N (%)	0.33±0.12	[0.12–0.74]	–	–	–
t2.12	Soil available nutrients (mg kg ⁻¹)					
t2.13	NH ₄ ⁺	30.7±29.1	[6.8–160.9]	0.32	–0.75	–0.30
t2.14	P	1.9±1.8	[0.2–8.9]	0.45	–0.64	–0.21
t2.15	Ca	2903±1749	[477–7925]	–0.86	–0.14	–0.09
t2.16	K	191±69	[89–419]	–0.39	–0.29	0.11
t2.17	Mg	261±100	[69–530]	–0.26	–0.60	–0.33

374 the relative abundance of the species “i” in the com-
 375 munity, and Trait_i is the average trait value obtained
 376 for this species “i” (Violle et al. 2007). The CWM
 377 values integrate the information on community struc-
 378 ture (local abundances of species) as well as on the
 379 functional identity of the dominant species. We have
 380 selected LMA_{CWM} and LDMC_{CWM} as the key function-
 381 al variables which better explain the response of the
 382 community to environmental factors (Garnier et al.
 383 2001).

384 Data analysis

385 A principal components analysis (PCA) of 20 leaf
 386 traits considered in this study (2 morphological, 16
 387 chemical, and 2 isotopic signatures) and 17 woody
 388 species (mean values of 5 individuals for each) was
 389 performed to better understand the multivariate patterns
 390 present in the data. Leaf thickness was excluded from
 391 the dataset for the multivariate analysis because meas-
 392 urements could not be obtained for some species with
 393 small-sized leaves. For comparison, a PCA analysis was
 394 also performed at the community level with the CWM
 395 values of 12 leaf traits (LMA, LDMC, isotopic signa-
 396 tures and macronutrient concentrations) for the 57 plots.

397 The bivariate relationships between species morpho-
 398 logical traits (LMA and LDMC) and the nutritional and

isotopic traits, previously averaged and log-transformed, 399
 were explored using standardised major axis slopes 400
 (SMAs, also known as reduced major axis slopes), a 401
 statistical tool highly recommended for allometric 402
 studies (Warton et al. 2006). SMA slopes are fitted 403
 by minimising the sums of squares of errors in X 404
 and Y dimensions simultaneously, and they show the 405
 proportional relationships between variables, i.e., how 406
 one variable scales against another. SMA regressions 407
 were performed using SMATR software ver. 2.0 (Falster 408
 et al. 2006). SMA fitting was also applied to explore the 409
 relationships between the same traits at the community 410
 level, considering the CWM at each sampling unit. The 411
 slope of the SMA regressions is of special interest, since 412
 it indicates the magnitude of the scaling between the 413
 variables. We only emphasized in the results section 414
 those relationships with an absolute value of the SMA 415
 slope higher than one. 416

417 We analysed the variation in CWMs of leaf traits in
 418 response to key environmental factors (bivariate rela-
 419 tionships), by means of Pearson correlation analyses.
 420 Specifically, we used light availability (GSF), soil
 421 water (annual average) and an integrated variable of
 422 nutrient availability, represented by a PCA factor cov-
 423 ering soil organic matter, and the concentrations of
 424 NH₄⁺, available P and available Mg (Table 2; scores
 425 of factor 2 were inversely transformed for clarity).

426 We controlled the increment of type I errors derived
 427 from multiple testing at the 5 % level using the ‘false
 428 discovery rate’ (FDR) procedure (Hochberg and
 429 Benjamini 2000), as suggested by García (2003).
 430 The corrected significance level was 0.031.

431 **Results**

432 Leaf trait variability among species

433 Across the studied species, there was a strong variability
 434 in the leaf traits; for example leaf mass per area varied
 435 twofold, from 60 gm⁻² (*Rubus ulmifolius*) to 151 gm⁻²
 436 (*Teline linifolia*) (Table 3). In general, micronutrients
 437 and non-essential elements exhibited a greater inter-
 438 specific variability than macronutrients; while among
 439 isotopic signatures, δ¹⁵N was more variable than δ¹³C
 440 (Tables S2, S3 and S4). The N isotopic composition was
 441 associated with the type of symbiotic/parasitic relation-
 442 ships of each species. Thus, N-fixing species (legumes)
 443 and the hemiparasitic species (*O. alba*) exhibited posi-
 444 tive values of δ¹⁵N, whereas the rest of species, which

445 had different mycorrhizal associations, showed negative
 446 δ¹⁵N values (Figure S1; mycorrhizal types according to
 447 Maremmani et al. 2003).

448 In the multivariate analysis of leaf traits (by PCA), the
 449 first axis (explaining a 26.2 % of the variance) was
 450 positively related to LMA, LDMC, C, the C:N ratio and
 451 δ¹³C, and negatively related to the leaf concentrations of
 452 all macronutrients (with the exception of P) and micro-
 453 nutrients (Fig. 1). The second PCA axis was most strongly
 454 correlated with the N-related variables, including N:P and
 455 δ¹⁵N, as well as the leaf Mn and Ni concentrations.
 456 Winter deciduous species (such as *C. monogyna*) and
 457 legume species (*C. villosa* and *T. linifolia*) were located
 458 towards the nutrient-rich (negative) end of axis 1, in
 459 contrast to species with higher δ¹³C and LMA values
 460 (higher than 100 gm⁻²), such as *Q. suber*, *P. lentiscus*
 461 and *P. latifolia*, which were located in the positive end.
 462 Symbiotically nitrogen fixing (legume) species, in par-
 463 ticular *C. villosa*, were separated at the negative end of
 464 axis 2 (Fig. 1). For this PCA analysis, samples of *O.*
 465 *alba* (hemiparasitic shrub) were excluded because their
 466 high concentration of P, Ca, Mg and S distorted the
 467 analysis (as found in a preliminary PCA, not shown).

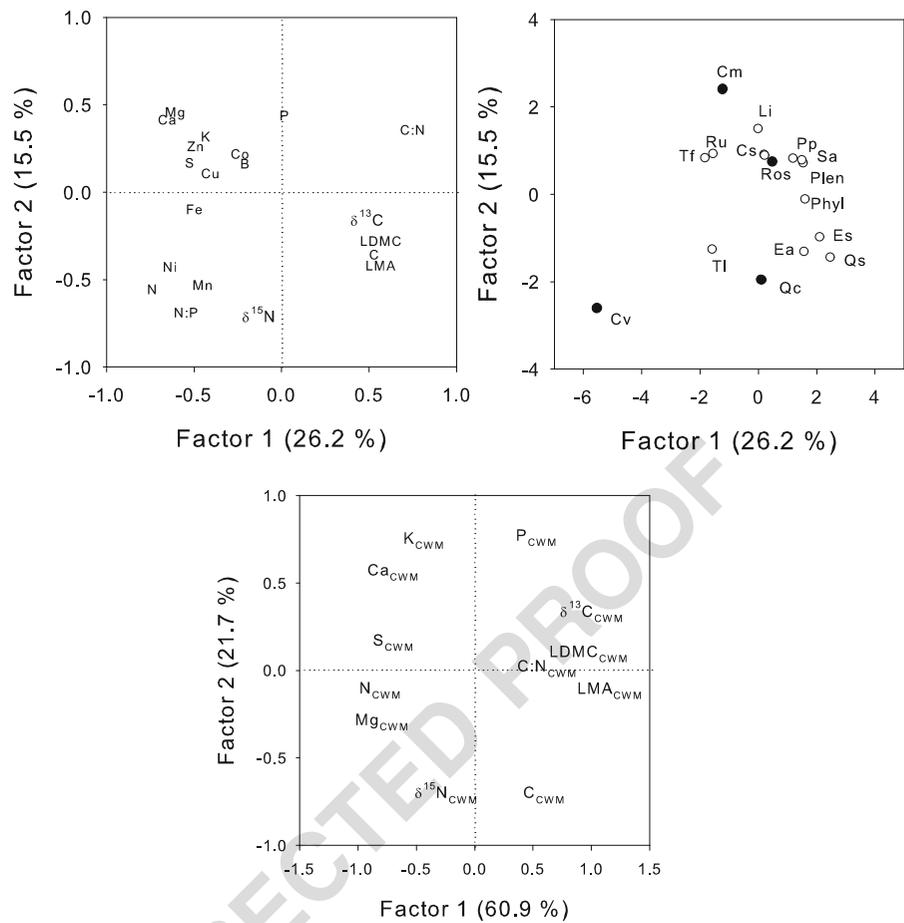
t3.1 **Table 3** Morphological leaf traits of the studied species (mean ± SD, n=5)

t3.2 Species	LMA (g m ⁻²)	LDMC (g g ⁻¹)	Leaf area (cm ²)	Thickness (mm)
t3.3 <i>C. monogyna</i>	73±26	0.35±0.1	4.14±1.75	0.23±0.03
t3.4 <i>C. salvifolius</i>	140±37	0.35±0.05	1.81±0.67	0.47±0.07
t3.5 <i>C. villosa</i>	72±12	0.24±0.01	1.12±1.04	na
t3.6 <i>E. arborea</i>	97±22	0.40±0.04	0.03±0.01	na
t3.7 <i>E. scoparia</i>	118±28	0.40±0.06	0.03±0.01	na
t3.8 <i>L. implexa</i>	92±22	0.31±0.05	9.14±1.59	0.30±0.04
t3.9 <i>O. alba</i>	115±31	0.30±0.03	0.75±0.32	na
t3.10 <i>P. latifolia</i>	122±29	0.46±0.04	5.55±1.20	0.26±0.04
t3.11 <i>P. lentiscus</i>	103±21	0.36±0.03	14.2±3.14	0.32±0.07
t3.12 <i>P. purpurea</i>	125±28	0.38±0.04	14.3±8.9	0.66±0.08
t3.13 <i>Q. canariensis</i>	116±20	0.46±0.02	20.7±10.5	0.32±0.05
t3.14 <i>Q. suber</i>	144±24	0.45±0.04	7.62±2.60	0.35±0.04
t3.15 <i>R. pouzinii</i>	68±5	0.39±0.01	23.3±4.2	0.18±0.01
t3.16 <i>R. ulmifolius</i>	60±5	0.40±0.03	43.7±9.20	0.27±0.06
t3.17 <i>S. aspera</i>	86±18	0.30±0.02	27.6±5.45	0.30±0.04
t3.18 <i>T. fruticans</i>	79±21	0.35±0.05	3.97±1.24	0.33±0.01
t3.19 <i>T. linifolia</i>	151±44	0.42±0.16	1.20±0.22	na
t3.20 Community CV (%)	34	21	119	38

na for these species, leaf thickness could not be obtained

LMA leaf mass per area; LDMC leaf dry matter content; CV coefficient of variation (sd/mean) × 100

Fig. 1 Ordination of leaf traits (*upper left*) and woody plant species (*upper right*) in the space defined by the first and second axes of principal component analysis (PCA). See species codes in Table 1. Open and filled circles correspond to evergreen and deciduous species, respectively. The comparative ordination of community-weighted leaf traits for 57 plots is showed in the lower panel (factor 2 has been rotated for clarity). LMA, leaf mass per area; LDMC, leaf dry matter content; $\delta^{13}\text{C}$, C^{13} abundance; $\delta^{15}\text{N}$, N^{15} abundance; C:N, carbon and nitrogen ratio; N:P, nitrogen and phosphorus ratio; CWM, community-weighted mean



468 At the community level, the first PCA axis was
 469 defined by a similar combination of leaf traits to that
 470 detected at the species level (Fig. 1), but with a much
 471 stronger explanatory power (61 % versus 26 % of the
 472 explained variance).

473 Links among leaf traits at the species
 474 and the community level

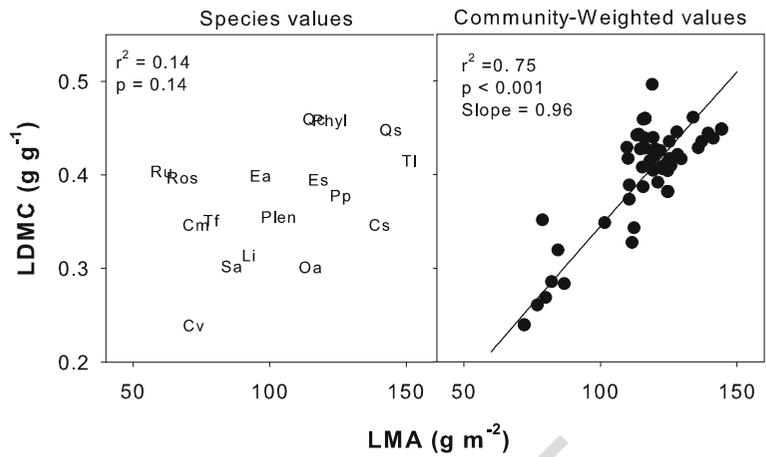
475 The relationships among leaf traits were not always
 476 consistent at the species and at the community level. In
 477 most cases, the relationships at the community were
 478 stronger than at the species level. For example, LMA
 479 and LDMC were positively and significantly related
 480 when community-weighted-means were considered,
 481 whereas no significant relationship was found in the
 482 cross-species analysis (Fig. 2). Interestingly, the rela-
 483 tionship between LMA and the isotopic signature of
 484 ^{13}C was positive and consistent at both levels, whereas
 485 for ^{15}N the relationship was non-significant at any level

(Fig. 3). The high values of the SMA slope for $\delta^{13}\text{C}$ 486
 (above 4 at the species level) indicated that higher LMA 487
 species were related with exponential increase in $\delta^{13}\text{C}$ 488
 and, thus, they were exponentially more efficient in their 489
 use of water than lower LMA species. 490

At the species level, LMA was not significantly rela- 491
 ted with N, P or any other nutrient, with the exception 492
 of Mg (Fig. 4 and Table S5). However, at the commu- 493
 nity level, LMA_{CWM} was negatively related with 494
 N, Ca and Mg concentrations with a SMA slope steeper 495
 than -1 , indicating a proportionally higher increase of 496
 nutrient concentration towards the low LMA end of the 497
 trait relationship (Fig. 4 and Table S5). 498

Bivariate relationships between LDMC and the nutri- 499
 ent variables followed the same pattern as with 500
 LMA. In general, very few significant relationships 501
 were found when species values were considered (only 502
 for Mg and Cu), while many of these relationships were 503
 significant when community-weighted values were used 504
 (Supplementary Material, Table S6). 505

Fig. 2 Relationship between leaf mass per area (LMA) and leaf dry matter content (LDMC), at the species (*left*) and at the community level (*right*), analysed by standardised major axis (SMA) regressions. See Table 1 for species codes. The SMA slope value is also indicated. See Table S5 for a complete report of the results of the bivariate correlations



506 Community-weighted means of leaf traits
507 and environmental factors

508 There was a great variation in the plant cover (repre-
509 sented by the total leaf area index, LAI) across the 57
510 sampled plots and, consequently, in the level of light
511 intercepted by the canopy (estimated as the global site

factor, GSF), which could be associated to a differential 512
distribution of woody plant species (Figure S2). 513
The explored gradient of plant cover ranged from open 514
shrublands (with LAI < 0.5 m² leaf per m² soil) domina- 515
ted by small-leaved species such as *C. villosa* 516
(72 % of cover) or *E. arborea* (17 %), to dense forests 517
(LAI of 2–3 m² m⁻²) with an overstorey of *Q. suber* 518

Fig. 3 Bivariate relationships between leaf mass per area (LMA), leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, at the species (*left*) and at the community (*right*) level, analysed by standardised major axis (SMA) regressions. See Table 1 for species codes. For those significant correlations, the SMA slope value is also indicated. See Table S5 for a complete report of the results of the bivariate correlations

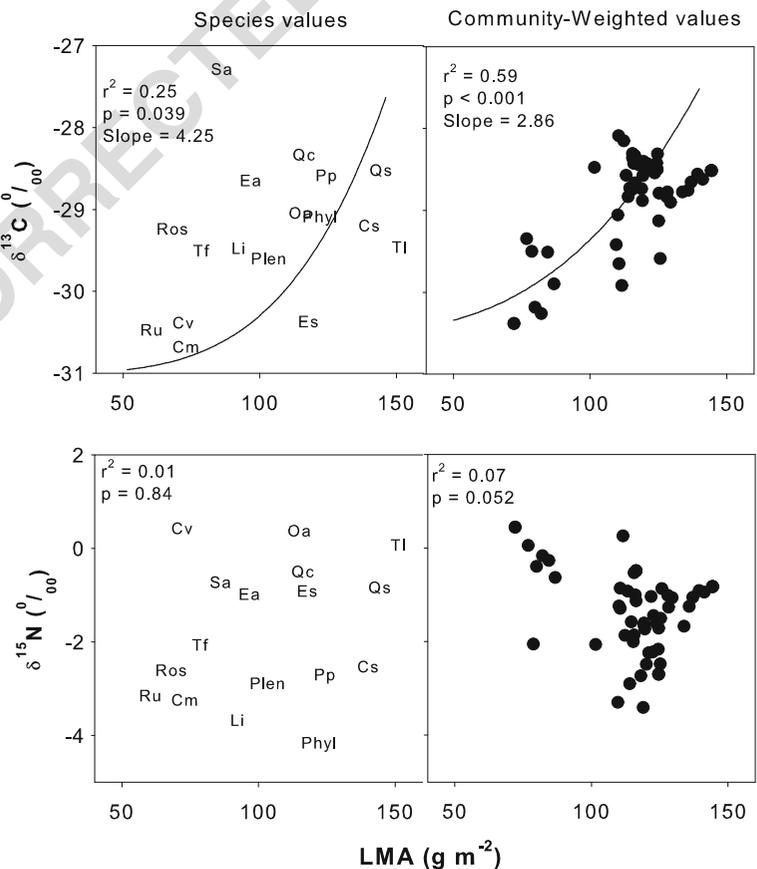
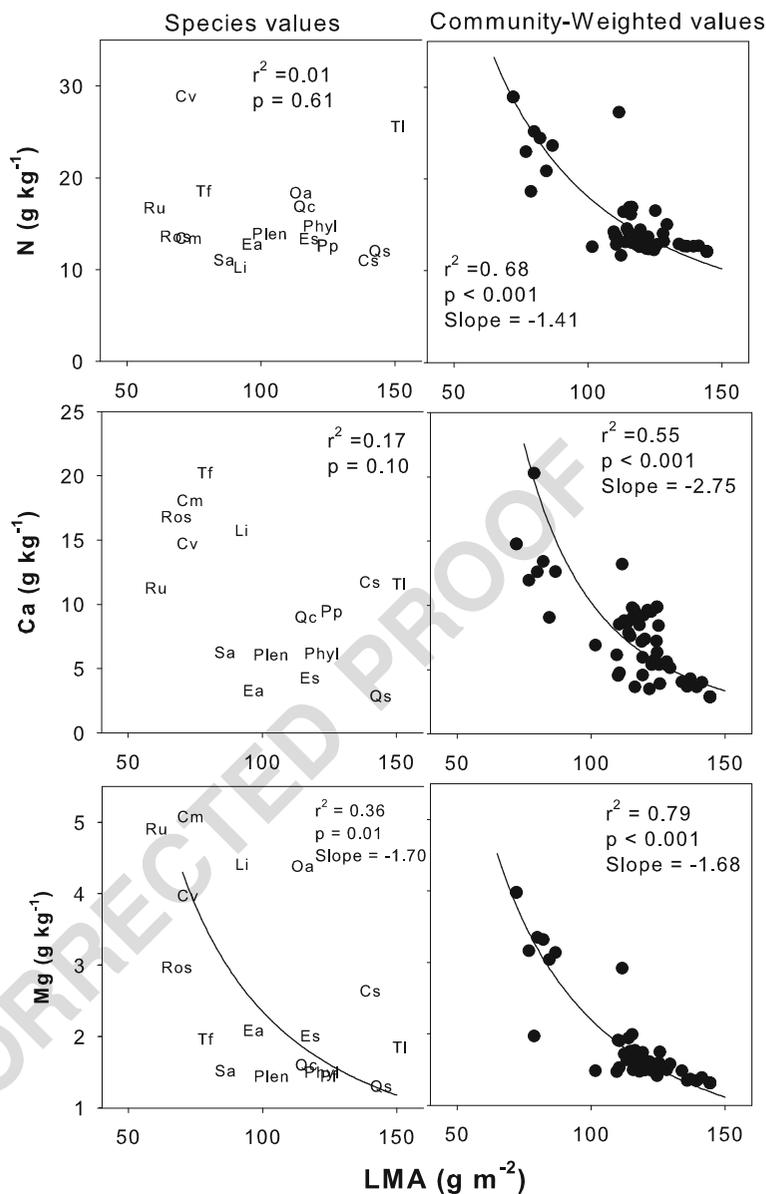


Fig. 4 Bivariate relationships between leaf mass per area (LMA) and leaf nutrient concentrations of N (top), Ca (centre) and Mg (bottom), at the species (left) and at the community (right) level, analysed by standardised major axis (SMA) regressions. See Table 1 for species codes. For significant correlations, the SMA slope value is also indicated. See Table S5 for a complete report of the results of the bivariate correlations



519 (14–23 %) and *Q. canariensis* (11–17 %) and a dense
 520 understorey of arborescent species such as *P. lentis-*
 521 *cus* (25–35 %), *P. latifolia* (8–16 %) and *E. arborea*
 522 (5–17 %).

523 The bivariate correlational analysis between the
 524 environmental factors and the studied leaf traits
 525 showed that light was the factor with the highest
 526 influence on the community-weighted-mean traits
 527 (Table 4). Unexpectedly, light availability was nega-
 528 tively related with both LMA_{CWM} and $LDMC_{CWM}$
 529 (Fig. 5), as well as with $C:N_{CWM}$ and $\delta^{13}C_{CWM}$. In
 530 contrast, light was positively correlated with both

N_{CWM} and $\delta^{15}N_{CWM}$. Soil moisture was only nega- 531
 532 tively related to C_{CWM} and $\delta^{13}C_{CWM}$, with no influ-
 533 ence on LMA_{CWM} or $LDMC_{CWM}$. Soil fertility
 534 (represented by a PCA factor, which integrates soil
 535 organic matter, and the availability of NH_4^+ , P and
 536 Mg, Table 2), was weakly related to the morphological
 537 traits (only a marginal positive relationship with
 538 $LDMC_{CWM}$), but more closely linked to some chemi-
 539 cal traits, such as N_{CWM} , $C:N_{CWM}$ and $\delta^{15}N_{CWM}$
 540 (Table 4). In general, when the average trait values
 541 for the species pool at each plot (without weighting by
 542 their relative abundance) were used the links between

t4.1 **Table 4** Results of the bivariate correlations between community-weighted-means traits and environmental factors

t4.2		LMA _{CWM}	LDMC _{CWM}	C _{CWM}	N _{CWM}	C:N _{CWM}	δ ¹³ C _{CWM}	δ ¹⁵ N _{CWM}
t4.3	LAI	0.49***	0.66***	0.31	-0.55***	0.47***	0.45***	-0.36**
t4.4	GSF	-0.63***	-0.78***	-0.32	0.66***	-0.56***	-0.53***	0.37**
t4.5	Soil pH	-0.08	-0.08	-0.39**	-0.03	-0.05	0.24	-0.22
t4.6	Soil organic matter	0.01	0.03	-0.27	-0.16	0.09	0.23	-0.39**
t4.7	Soil total N	-0.01	0.03	-0.20	-0.16	0.09	0.21	-0.34**
t4.8	Soil NH ₄ ⁺	0.18	0.16	0.08	-0.20	0.19	0.14	-0.09
t4.9	Soil P	0.32	0.28	0.23	-0.23	0.25	0.09	0.02
t4.10	Soil Ca	0.02	-0.05	-0.39**	-0.13	0.05	0.32	-0.33
t4.11	Soil K	0.08	-0.05	-0.17	-0.16	0.15	0.19	-0.15
t4.12	Soil Mg	0.23	0.26	-0.18	-0.21	0.11	0.29	-0.14
t4.13	Soil Fertility Index (PCA Factor)	0.25	0.28*	0.07	0.37**	0.31*	0.39**	0.37**
t4.14	Spring soil moisture	-0.16	-0.20	-0.37**	0.01	-0.06	0.25	-0.12
t4.15	Summer soil moisture	-0.04	-0.02	-0.37**	-0.12	0.02	0.35**	-0.22
t4.16	Annual mean soil moisture	0.06	0-11	0.47**	0.05	0.14	0.13	0.24

Bold characters indicate significant values after controlling for the false discovery rate (significance levels are * $p < 0.031$; ** $p < 0.01$; *** $p < 0.001$)

LMA leaf mass per area; LDMC leaf dry matter content; GSF global site factor; LAI leaf area index

543 LMA, LDMC and the environmental variables were
 544 similar (Fig 5), although the explanatory power of the
 545 relationships was higher for the CWM-values.

546 **Discussion**

547 Links among functional leaf traits at the species
 548 and community levels

549 *Are LMA and LDMC related to plant nutrient*
 550 *economy?*

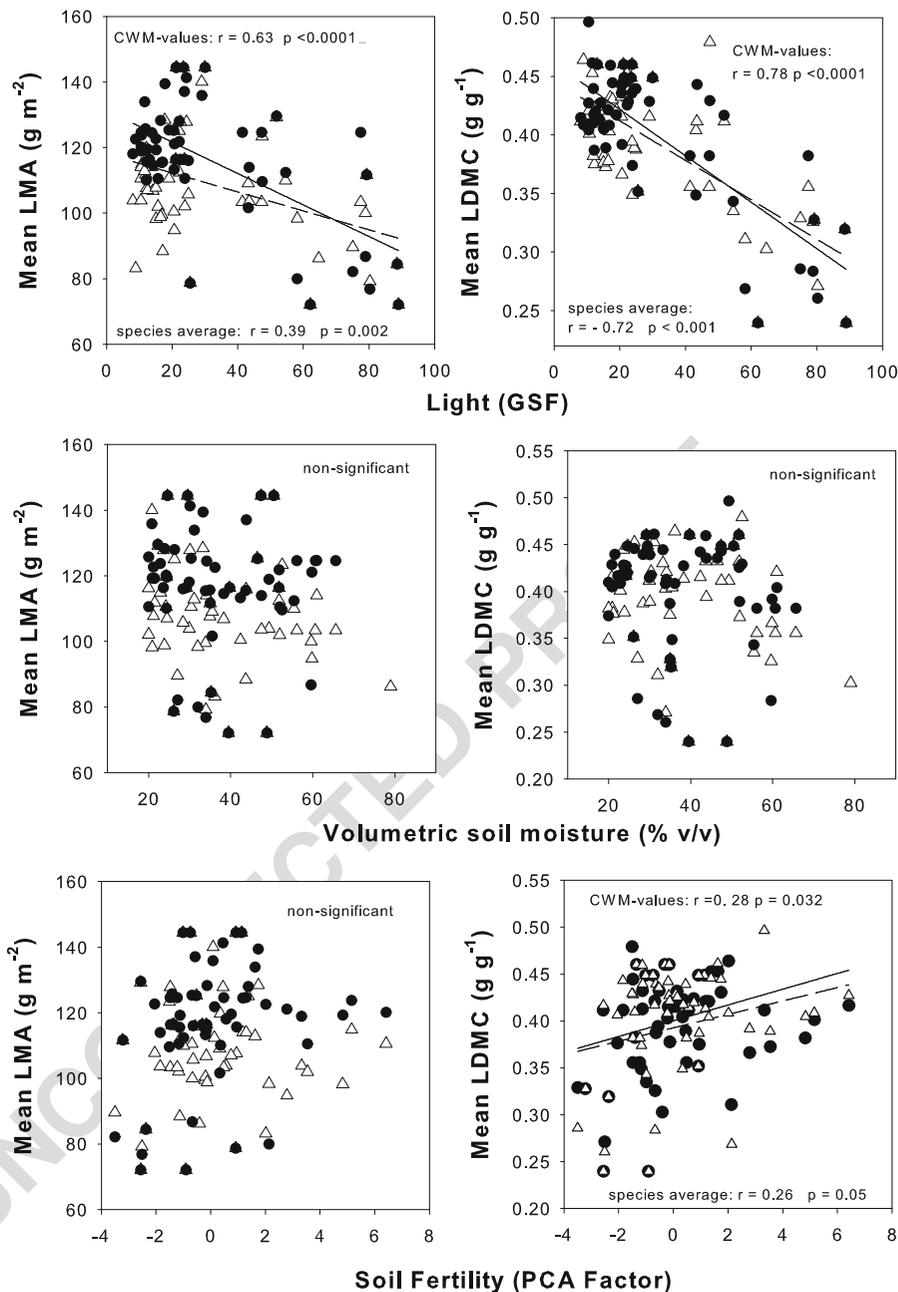
551 Mediterranean ecosystems provide excellent sites
 552 where exploring the relationships among functional
 553 traits. The small-scale heterogeneity in the conditions
 554 of irradiance and the usual concurrence of water and
 555 nutrient limitations in these systems may promote the
 556 coexistence of different species with a wide range of
 557 LMA values (Poorter et al. 2009). In the studied forest,
 558 LMA values ranged from 64 to 151 gm⁻², which is the
 559 common range for Mediterranean woody plant spe-
 560 cies (Galmés et al. 2007; Hernández et al. 2010;
 561 Mediavilla et al. 2008; Paula and Pausas 2006;
 562 Villar and Merino 2001). Chemical traits were especial-
 563 ly variable, including the isotopic signatures; nitrogen
 564 isotopic signature differed among functional groups of

565 symbiotic interactions and, thus, could be used as 565
 566 a possible marker for mycorrhizal habit (Högberg 566
 567 1990). 567

568 All these chemical and morphological traits showed 568
 569 a strong multivariate covariation, especially at the 569
 570 community level, which can be used to characterize 570
 571 different plant functional groups. The main variation 571
 572 trend was associated with the acquisition-conservation 572
 573 trade-off (Diaz et al. 2004) and confirmed the role of 573
 574 LMA and LDMC as indicators of differential func- 574
 575 tional strategies. Thus, communities with a predomi- 575
 576 nant conservative strategy exhibited high values of 576
 577 LMA and LDMC, positively associated to C concen- 577
 578 tration, C:N ratio (sclerophyllous type) and high water 578
 579 use efficiency (high δ¹³C values). On the contrary, com- 579
 580 munities with a predominant resource-acquisition strat- 580
 581 egy showed a lower water-use efficiency (low δ¹³C) and 581
 582 low LMA and LDMC (Poorter and Garnier 1999; 582
 583 Wright and Westoby 2001). 583

584 The bivariate analyses confirmed that the links 584
 585 between the leaf morphological and the leaf nutritional 585
 586 traits are much weaker at the species than at the 586
 587 community level. Thus, our first hypothesis was not 587
 588 supported for the species pool (species mean values), 588
 589 but it was when considering the relative abundance of 589
 590 the dominant species constituting the community 590
 591 (community-weighted-means). 591

Fig. 5 Relationship between main environmental gradients (light, water and soil fertility) and community leaf mass per area (LMA), and leaf dry matter content (LDMC). Closed circles and solid lines correspond to the community-weighted means (CWM, weighting by the relative abundance of the species in the community), while open triangles and dashed lines corresponds to the un-weighted trait values (average of present species). Light availability was estimated by global site factor (GSF), soil moisture was calculated as the annual average, and soil fertility was represented by a PCA factor integrating soil organic matter and the availability of NH_4^+ , P and Mg



592 At the species level, LMA or LDMC were not related
 593 to almost any nutrient concentration, not even to those
 594 elements included in the nucleic acid-protein set (N, P,
 595 Cu, S, Fe, Garten 1978). These results contrast with the
 596 consistently negative relationship between LMA and
 597 both N and P concentrations that has been reported for
 598 global datasets (Liu et al. 2010; Ordoñez et al. 2009;
 599 Wright et al. 2004a, 2005), and thus, indicates that
 600 global patterns may not hold at some local scales.

601 While trait relationships can be considered very
 602 general, they are not necessarily universal (Wright et
 603 al. 2005). The specific environmental conditions in
 604 each site may play a central role in the strength of
 605 the leaf morphology vs. nutrient relationships. Recent
 606 analyses by Freschet et al. (2011) have shown that as
 607 much as a 50 % of the global variability in SLA and
 608 leaf N occurs within communities, which may be
 609 caused by large differences in the nature and strength

of abiotic and biotic drivers of dominant species assembly at local scales. Within the worldwide LMA spectrum, Mediterranean species have low SLA (and therefore high LMA), and comparatively high N concentrations (Freschet et al. 2011), which is known to enhance water conservation during photosynthesis in species from low-rainfall sites (Wright and Westoby 2002). In some P-limited ecosystems, as the studied forest, leaf morphology and N concentrations are usually unrelated, and LMA and net photosynthetic capacity may be more closely linked to P (Niinemets and Kull 2003; Liu et al. 2010; Chen et al. 2011). In this study, however, we did not find significant links between LMA and leaf phosphorous at the species or at the community level.

If the strength of the links between LMA and leaf nutrients depends on the relative availability of the most limiting element (Niinemets and Kull 2003), then we could conclude that Mg is the most limiting nutrient in the studied system, given the consistent negative relationship between Mg and LMA at both levels of analysis. Among the studied species, leaf Mg ranged from 1.3 to 5.1 g kg^{-1} , with a coefficient of variation higher than 50 % (Table S2) probably reflecting large among-species differences in the requirements for this essential element. The links between LMA and leaf Mg (which is a structural component of the chlorophylls and essential for photosynthesis) remain largely untested both at the local and at the global scales (but see Fyllas et al. 2009).

Potassium was neither related to LMA. In the leaf, this element has a less structural function than N or Mg, as is mainly found as a dissolved ion, contributing to the leaf osmotic regulation and to the activation of many photosynthetic enzymes. Despite in some local studies leaf K is significantly linked to LMA (Niinemets and Kull 2003; Fyllas et al. 2009), global data sets have shown that this element is very weakly related to LMA, in comparison to N and P (Wright et al. 2005).

The range of growth forms and trait variation in this study may also explain the discrepancies with the global patterns for the LMA vs. nutrient relationships. We focused here on woody plant species, which have a much greater proportion of biomass in non-productive tissues than herbaceous plants. The partitioning of nutrients among the different plant tissues at the whole-plant level may mask the nutrient-LMA relationships for a set of woody plants, in comparison

to broader data sets including different growth forms. To detect broad trait relationships among species, the range of trait variability must be large, at least of one order of magnitude (Wright et al. 2004b). Based in this data set it can be concluded that, within the normal range of LMA values for Mediterranean woody plants, and despite N and P values ranged 2.6 and 3.8-fold, respectively, the links between LMA and N or P among species are weak.

Interestingly, N and P were partly uncoupled at both levels of analysis, located in opposite positions in the PCA-axes, contrasting to the global trend of positive correlation between these two nutrients (Wright et al. 2004a). Again, local data set may not support the global general relationships between traits (Wright et al. 2005). This uncoupling may be driven by the plant-microbial interactions, which are especially relevant in these nutrient-poor soils. Phosphorous availability is very low in comparison to N availability, as revealed by the general high N:P ratios in the leaves (>20) of the studied plants. In these situations, the type of mycorrhizal interaction may play a central role in the community assembly. For example, Pekin et al. (2011) have shown that, in some Mediterranean forest ecosystems, the distribution of root traits (including the type of symbiotic interactions) is driven by the N to P availability ratio in the soil. Ectomycorrhizal, non-mycorrhizal and ericoid mycorrhizal species have a competitive advantage over arbuscular species at sites with low N fertility where P is not limiting. According to our data, N-fixation, which promotes a high N leaf concentration, does not seem to promote also a high P-uptake in the studied species. Actually, plants with higher P leaf concentrations tended to have lower $\delta^{15}\text{N}$, which characterized arbuscular and ectomycorrhizal associations.

Despite that leaf ^{15}N discriminated among mycorrhizal groups, the hypothesis that plant species with low LMA (and presumably a resource-acquisition strategy) have a low dependence on mycorrhizal interactions for N-uptake (i.e., higher leaf ^{15}N values) was not supported by our data. In contrast, the hypothesis expecting a positive relationship between LMA and $\delta^{13}\text{C}$ was supported at both the species and the community level, in accordance with the strong association of LMA with plant water-use efficiency reported in previous studies (Cunningham et al. 1999; de Bello et al. 2009).

708 *Are LMA and LDMC relationships consistent*
 709 *at the species and community levels?*

710 The links between the morphological (LMA and
 711 LDMC) and the chemical traits were stronger at the
 712 community level. By the community-weighted mean
 713 analysis the environmental filters are, somehow, taken
 714 into account, since they determine how species replace
 715 each other, and thus, how different the weighted averages
 716 are across the studied plots. This strong correlation
 717 among traits at the community level suggests that:
 718 i) those traits have parallel shifts along the environ-
 719 mental gradients that determine such community as-
 720 sembly, even though these traits are independent when
 721 the individual taxa are considered, and ii) the func-
 722 tional structure of the studied forest communities is
 723 driven not only by species identity but also by their
 724 relative abundances within the community. Other stud-
 725 ies have also found differences in trait relationships
 726 depending whether the species values or the commu-
 727 nity averages were used. In a Mediterranean chaparral
 728 of California, Ackerly et al. (2002) obtained stronger
 729 links between leaf size and specific leaf area, as well
 730 as a stronger response of the leaf traits to insolation,
 731 when using weighted averages compared to the cross-
 732 species analyses. For a set of perennial species from
 733 Australia, Fonseca et al. (2000) also found that some
 734 leaf traits were not related across-species, but converged
 735 along gradients of rainfall and soil phosphorus. Potential
 736 limiting resources may act as the environmental filters
 737 promoting the convergence of traits related to acquisi-
 738 tion/conservation of resources (Cornwell and Ackerly
 739 2010; Sonnier et al. 2010). In this study, the consistent
 740 strong links between light availability (main environ-
 741 mental gradient) and the most important leaf traits
 742 (LMA, LDMC, N and C:N) support the convergence
 743 of independently-related traits.

744 LMA and LDCM relationships with environmental
 745 filters

746 Which are the environmental factors that determine
 747 the convergence of the leaf traits, and thus, the func-
 748 tional structure in the community?

749 Among the studied environmental factors, light
 750 availability at the understorey had the strongest rela-
 751 tionship with both morphological (LMA_{CWM} and
 752 LDMC_{CWM}) and chemical traits (N, C:N, $\delta^{13}\text{C}$ and
 753 $\delta^{15}\text{N}$ community-weighted means). Interestingly, light

availability was negatively related with leaf LMA_{CWM} 754
 and LDMC_{CWM} (Table 4), contrary to our initial hy- 755
 pothesis. The results were similar when species aver- 756
 ages (without weighting by the relative abundance) 757
 were used, although with a lower explanatory power. 758
 The contrasting plant composition in the community 759
 along the light gradient determined this pattern. On 760
 one side of the gradient, woody plant species with 761
 sclerophyll leaves (higher values of LMA, LDMC 762
 and C:N) and arbuscular and ericoid mycorrhizae 763
 (low foliar $\delta^{15}\text{N}$) tend to form denser forests and a 764
 shadier understorey, and to exclude juvenile light- 765
 demanders (Canham et al. 1994; Sack et al. 2003). 766
 On the other side, open microsites are dominated by a 767
 legume shrub (*C. villosa*) with the drought-avoidance 768
 strategy (de Lillis and Fontanella 1992) of summer- 769
 deciduous leaf habit (lower LMA and LDMC) and 770
 symbiotic N-fixation ability (higher $\delta^{15}\text{N}$ and lower 771
 C:N). This species was not present in the plots with 772
 lowest light availability within the forest (Figure S2). 773
 Woody legumes tend to have a reduced shade toler- 774
 ance, and are rarely found (excepting in tropical for- 775
 ests) in closed canopy systems (Vitousek et al. 2002). 776
 This successful combination of traits (summer leaf 777
 fall, short leaf life-span, low LMA and high leaf N 778
 concentration) characterises the dominant plant spe- 779
 cies in some dry, highly exposed microsites under 780
 Mediterranean climate (Westman 1981), and repre- 781
 sents the functional strategy of several opportunistic 782
 woody Mediterranean species in canopy gaps follow- 783
 ing a perturbation (Ackerly 2004). Therefore, the ob- 784
 served reduction of LMA and LDMC with light 785
 availability is mainly driven by the presence and 786
 dominance of these deciduous legume shrub spe- 787
 cies in the gaps, and may not be applicable to 788
 other forest ecosystems. This pattern also suggests 789
 that, along this environmental gradient, light avail- 790
 ability filters both the presence and the dominance 791
 of the species in a similar manner, that is, select- 792
 ing a reduced number of species with certain traits 793
 in the most exposed sites. Since light availability 794
 was the environmental factor most closely related 795
 to the dominance of the different functional traits, 796
 including the chemical traits, perturbations of can- 797
 opy conditions (and hence in light availability) 798
 may lead to changes in the LMA and LDMC of the 799
 dominant woody species, with important consequences 800
 for the biogeochemical cycles of C and N, and also of 801
 Mg, Ca, K and S. 802

803 In spite of the widely recognised importance of soil
 804 water as a main limiting resource for plants in
 805 Mediterranean conditions, we did not find any signif-
 806 icant relationship between this soil factor and the
 807 LMA_{CWM} at the forest stand scale explored. Thus,
 808 the results did not support our hypothesis that this
 809 factor acts as the main environmental filter. This con-
 810 trasts with previous studies (of grassland communities)
 811 where community-weighted LMA clearly responded to
 812 soil moisture or flooding gradients (Cingolani et al.
 813 2007; Jung et al. 2010). The lack of relationships be-
 814 tween soil moisture and leaf traits may be determined by
 815 the concurrence of contrasting leaf strategies in the
 816 driest end of the gradient, that is both summer deciduous
 817 (low LMA) and sclerophyll evergreen (high LMA) spe-
 818 cies can coexist in the driest plots within the forest.
 819 Thus, soil moisture could promote the divergence, rather
 820 than the convergence of traits in the community. On the
 821 other hand, Ackerly (2004) showed that, for a range of
 822 Mediterranean woody species, minimum seasonal leaf
 823 water potential (an indicator of water stress) was related
 824 to wood density, vessel diameter, twig width, and leaf
 825 area:sapwood area ratios, but not to leaf life span (which
 826 is closely linked to LMA). Pekin et al. (2009) also found
 827 a high correlation between water availability and leaf
 828 area:sapwood area ratio in Mediterranean forest ecosys-
 829 tems. For a complete understanding of the response of
 830 this woody plant community to soil moisture further
 831 investigations focused on root and wood traits are
 832 needed.

833 Despite some recent studies have shown that soil
 834 fertility may be the environmental factor with the
 835 highest influence on leaf traits at the global (Ordoñez
 836 et al. 2009) and at regional scales (Fyllas et al. 2009),
 837 in this forest ecosystem the soil fertility had no signif-
 838 icant influence on LMA_{CWM} of woody species. It had
 839 some influence on $LDMC_{CWM}$, although the explana-
 840 tory power of this relationship was very low ($r^2 =$
 841 0.09), much lower than that of the relationship be-
 842 tween light and LDMC ($r^2 = 0.61$). Nutrient limitations
 843 are more likely to influence LMA through changes in
 844 the leaf density (Poorter et al. 2009). Since LDMC and
 845 leaf density are highly correlated (Hodgson et al.
 846 2011) a subtle influence of soil fertility could be more
 847 likely reflected on LDMC than on LMA variation. In
 848 this forest site, light and soil fertility gradients are
 849 linked and opposed; thus open, disturbed sites are usu-
 850 ally nutrient-poor while P availability largely depends
 851 on the litter supplies from oak species in the shaded

understorey (García et al. 2006). In this situation, LMA, 852
 which is largely influenced by light conditions, may 853
 discriminate better among communities than LDMC 854
 (Hodgson et al. 2011). The links between soil fertility 855
 and leaf traits found in this study, although weak, also 856
 reflected the contrasting plant composition along the 857
 environmental gradient. Soil fertility was positively 858
 linked to LDMC, C:N and $\delta^{13}C$, and those open, less 859
 fertile sites were dominated by *Calicotome villosa*, the 860
 summer-deciduous species with the lowest LDMC and 861
 the highest leaf N values in the community. 862

In conclusion, our study showed that LMA and 863
 LDMC were significantly related to many other chemi- 864
 cal leaf traits (nutrient concentrations), but only when 865
 using abundance-weighted values (that is, at the com- 866
 munity level). Thus, most of the leaf traits have paral- 867
 lel shifts along the environmental factors that 868
 determine the community assembly, even if they are 869
 independent or weakly related across individual taxa. 870
 Light availability was the main environmental factor 871
 determining this convergence of the community leaf 872
 traits, with no apparent influence of soil moisture on 873
 leaf traits (at the studied stand level) despite the im- 874
 portance of water in these drought-prone ecosystems. 875
 876

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