

1 **Relationships between leaf morphological traits, nutrient**
2 **concentrations and isotopic signatures for Mediterranean woody plant**
3 **species and communities**

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27 **Abstract**

28 *Background and Aims.* Soil factors are driving forces that influence spatial distribution
29 and functional traits of plant species. We test whether two anchor morphological traits -
30 leaf mass per area (LMA) and leaf dry matter content (LDMC) - are significantly related
31 to a broad range of leaf nutrient concentrations in Mediterranean woody plant species.
32 We also explore the main environmental filters (light availability, soil moisture and soil
33 nutrients) that determine the patterns of these functional traits in a forest stand.

34 *Methods.* Four morphological and 19 chemical leaf traits (macronutrients and trace
35 elements and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures) were analysed in 17 woody plant species.
36 Community-weighted leaf traits were calculated for 57 plots within the forest. Links
37 between LMA, LDMC and other leaf traits were analysed at the species and the
38 community level using standardised major axis (SMA) regressions.

39 *Results.* LMA and LDMC were significantly related to many leaf nutrient
40 concentrations, but only when using abundance-weighted values at community level.
41 Among-traits links were much weaker for the cross-species analysis. Nitrogen isotopic
42 signatures were useful to understand different resource-use strategies. Community-
43 weighted LMA and LDMC were negatively related to light availability, contrary to
44 what was expected.

45 *Conclusion.* Community leaf traits have parallel shifts along the environmental factors
46 that determine the community assembly, even though they are weakly related across
47 individual taxa. Light availability is the main environmental factor determining this
48 convergence of the community leaf traits.

49

50 **Keywords** Community weighted means • Functional traits • Leaf dry matter content •

51 Leaf mass per area • Macronutrients • Specific leaf area • Isotopes

52

53

54 **Introduction**

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

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

78 Cross-species analyses at global-scale have demonstrated that LMA, N and P
79 leaf concentrations, and photosynthetic capacity are strongly inter-correlated (Poorter et
80 al. 2009; Wright et al. 2004a). However, multivariate analyses of leaf composition have
81 shown that the N and P variation trend (so-called nucleic acid-protein set of elements)
82 differs from the trend for other elements such as Ca, K and Mg, which have
83 predominant structural and enzymatic functions (Aponte et al. 2011; Garten 1978;
84 Watanabe et al. 2007). The differences among species in nutrient requirements, not only
85 of N and P, but also of Ca, K, Mg and micronutrients such as Mo, Fe and Cu, may
86 favour their coexistence by separation of their biogeochemical niches (sensu Peñuelas et
87 al. 2008, 2011).

88 Although most studies have used LMA as the anchor trait (sensu Ackerly 2004),
89 leaf dry matter content (LDMC, dry leaf mass per water-saturated fresh leaf mass) has
90 proved to be equally or more important trait. LDMC is linked to the leaf protein
91 concentration and cytoplasmic volume, and therefore to plant metabolism (Wilson et al.
92 1999). It can determine the aboveground primary productivity and the digestibility of
93 the leaf (Pontes et al. 2007), the decomposability of the litter (Garnier et al. 2004), and
94 sometimes it can be better correlated with soil fertility than LMA (Hodgson et al. 2011;
95 Rusch et al. 2009). However, very few works have analysed the relationships between
96 LDMC and a broad range of leaf nutrient concentrations.

97 Isotopic signatures (expressed as N and C isotope ratios) also provide useful
98 information to characterize different strategies of resource acquisition in plants. The leaf
99 N isotopic signature integrates different factors involved in N acquisition, such as the
100 source and the soil depth from which N is taken up, the association with mycorrhizal
101 and symbiotic microorganisms, and the within-plant processes of N transport and
102 assimilation (Högberg 1997). The type of mycorrhizal interaction largely explains the

103 differences in $\delta^{15}\text{N}$ among plants at a global scale (Craine et al. 2009), as well as among
104 coexisting species at the community scale (Hobbie et al. 2000). Ericoid and
105 ectomycorrhizal strategies, which are usually related to low leaf $\delta^{15}\text{N}$ values (Craine et
106 al. 2009; Kranabetter and MacKenzie 2010), are linked to resource-conservation
107 attributes, such as low plant growth rates, low foliar nutrient concentrations and poor
108 litter decomposability (Cornelissen et al. 2001; Meers et al. 2010). Negative $\delta^{15}\text{N}$ values
109 in leaves may be indicative of a high dependence on mycorrhizal interactions for N
110 uptake, which is increased under low soil N availability (Hobbie et al. 1999, 2000). The
111 linkages between leaf $\delta^{15}\text{N}$ values and other leaf traits remain largely untested. In
112 contrast, the well-known relationship between $\delta^{13}\text{C}$ and water use efficiency (Farquhar
113 et al. 1989) has promoted the frequent use of this isotopic signature to detect functional
114 trait syndromes (e.g., Escudero et al. 2008; Lamont et al. 2002).

115 Most studies on leaf traits have been carried out at the species level (by
116 comparing simple averages of traits by species). To scale up from the species to the
117 community level, recent studies have incorporated the use of community-weighted-
118 means (Díaz et al. 2007; Violle et al. 2007), where functional traits are weighted by the
119 relative abundance of each of the dominant constituting species. These community-
120 aggregated values are particularly helpful to study the response of traits to
121 environmental factors, and to explore the links between traits and ecosystem processes
122 and services (Garnier et al. 2004). The environmental factors determine how species
123 replace each other, and thus, how different the weighted averages are across the studied
124 plots. A close link between traits at the community level would suggest that the
125 environmental filters that determine such community assembly promote the
126 convergence of certain individual traits in that community. Since dominant species tend
127 to have leaf trait values better linked to their environments than less abundant species,

128 we expect to find stronger associations among traits and clearer response of traits to
129 environmental factors when using the abundance-weighted approach, rather than when
130 using the average trait value for the species pool in the community (Ackerly et al. 2002;
131 Cingolani et al. 2005, 2007).

132 In this study we explored the spectrum of leaf traits (mainly LMA and LDMC)
133 and their relationships with nutrient concentrations and isotopic signatures in a
134 Mediterranean woodland, testing these relationships at both the species and the
135 community level. We pursued two particular objectives: first, we analysed the
136 relationships between LMA, LDMC and several nutritional traits: leaf concentrations of
137 macro- and micronutrients, non-essential trace elements, and C and N isotopes. Our
138 hypothesis was that species with a marked resource-acquisition strategy (i.e., with low
139 values of LMA) will exhibit: i) higher nutrient leaf concentrations, especially for those
140 nutrients with a prevalent photosynthetic function; ii) a lower dependence on
141 mycorrhizal interactions for N-uptake (i.e., higher leaf ¹⁵N values); and iii) a reduced
142 water-use efficiency (i.e., lower ¹³C values). We tested whether the links among traits at
143 the species level (which would reflect the evolutionary covariation of traits in a species
144 pool) are similar to those links at the community level (which would reflect the
145 convergence of traits promoted by the environmental filters).

146 Second, we studied the changes in community weighted and unweighted means of
147 LMA, LDMC and nutrient-related leaf traits along a broad and heterogeneous range of
148 environmental conditions in order to identify the main abiotic factors structuring those
149 patterns (light, soil water and soil fertility). The general hypothesis here was that the
150 dominance of the species in the community is more strongly filtered by the abiotic
151 factors than the presence/absence of individual taxa in a species pool. Thus the
152 abundance-weighted traits are expected to show higher relationships with the

153 environmental factors than the unweighted (based on presence/absence) traits. In
154 particular, the community-weighted LMA and LDMC values are expected to decrease
155 with increasing forest canopy density (lower light) as well as with increasing nutrient
156 and water availability in soil, due to a higher proportion of species with a predominant
157 resource-acquisition strategy.

158 **Material and Methods**

159 Study area, species selection and sampling design

160

161 The study area is located in the Aljibe Mountains, a protected mixed oak forest area in
162 southern Spain. The climate is of a sub-humid Mediterranean type with mild, wet
163 winters alternating with hot, dry summers and most rainfall (95%) occurring from
164 October to May. The bedrock is dominated by Oligo-Miocene sandstone and produces
165 acidic, nutrient-poor soils, which are frequently interspersed with layers of marl
166 sediments, yielding soils richer in clay (*Haploxererts*, Soil Survey Staff 2006). The
167 vegetation is dominated by the evergreen cork oak (*Q. suber* L.) mixed with the winter-
168 deciduous Algerian oak (*Q. canariensis* Willd.), which is locally abundant in the valley
169 bottoms (Urbieta et al. 2008). The study was conducted in a forest stand (La Saucedá;
170 36° 31' 54''N, 5° 34' 29'' W) located at an altitude of 530-560 m on a NW facing slope.
171 The mean annual temperature is 15.5° C, and the mean annual rainfall is 1470 mm. Tree
172 density in the stand is relatively low, with 219 stems ha⁻¹ and a basal area of 22 m² ha⁻¹
173 (see more details about the forest site in Pérez-Ramos et al. 2008 and Quilchano et al.
174 2008).

175 To represent the dominant vegetation of the studied mixed-oak forest, we selected
176 seventeen woody plant species, including the dominant oak tree species (*Q. suber* and
177 *Q. canariensis*) and the most abundant shrubs and vines in the understorey (Table 1).

178 They were also selected to cover the widest variability of leaf traits in the area.
179 Nomenclature follows Valdés et al. (1987), with exception of *Teline linifolia* (Talavera
180 and Gibbs, 1999). In late spring 2008, during the peak of vegetative growth, 32 plots
181 (3×3m) were set up within the forest site covering a wide range of environmental
182 conditions. In each plot, one healthy adult of each of the most dominant woody plant
183 species was collected for leaf trait measurements, making a total of 85 individuals (five
184 per species) distributed among the 32 plots. For each selected individual, we collected at
185 least two branches with young, fully expanded leaves from those parts of the plant with
186 the highest light exposition. The branches were placed in plastic bags and transported in
187 a chilled, dark container to the laboratory, where the plants were stored in darkness at
188 15°C with the stem bases submerged in water for at least 12 h to fully rehydrate the
189 leaves.

190 Each of these 32 plots was characterised by analysing soil samples (0-25 cm
191 depth) for physical and chemical properties. Soil texture was determined by the
192 Bouyoucos hydrometer method; pH was measured in a 1:2.5 soil:water suspension; soil
193 organic matter was determined by combustion at 450 °C and total N was determined by
194 Kjeldahl digestion. Available P was estimated by the Bray method; Ca, K and Mg were
195 extracted with 1 M ammonium acetate and determined by atomic absorption
196 spectrophotometry. The availability of micronutrients (Cu, Fe, Mn and Zn) and S was
197 determined using an EDTA solution and analysed by ICP-OES (inductively coupled
198 plasma optical emission spectrophotometry; Thermo Jarrell Ash Corporation, Franklin,
199 Massachusetts, USA). See details on methods for soil analyses in Sparks (1996) and a
200 data summary in Table S1.

201

202 Leaf trait measurements

203

204 *Morphological traits.* All leaf measurements were conducted following the criteria
205 defined by Cornelissen et al. (2003). Five rehydrated and fully expanded young leaves
206 per individual were harvested and weighed to obtain the lamina and petiole fresh mass.
207 Leaf thickness (average of three measurements per leaf) was measured with a
208 micrometer (Electronic Digital Micrometer Comecta SA, Barcelona, Spain). For five of
209 the seventeen selected species (*C. villosa*, *E. arborea*, *E. scoparia*, *O. alba* and *T.*
210 *linifolia*), leaf thickness could not be measured because of their small leaf size. Fresh
211 leaves were scanned, and leaf area was determined by digital analysis of the images
212 using specific software (Image-Pro Plus 4.5, Media Cybernetic Inc. USA). Finally, the
213 leaves were oven-dried at 70 °C for 48 h and then weighed to the nearest 0.0001 g.

214 The leaf mass per area (LMA, g m⁻²) was calculated as the ratio between the dry
215 mass of the lamina and its area. Likewise, the leaf dry matter content (LDMC, g g⁻¹)
216 was calculated as the ratio between the dry and the fresh (saturated) weights of the
217 lamina.

218 *Chemical traits.* Additional leaves were collected from each individual (from the
219 outer part of the crown) for chemical analysis. The laminas of the leaves were separated,
220 oven-dried (at 70 °C for 48 h) and ground using a stainless steel mill. The leaf carbon
221 concentration was determined in an elemental analyser (CHNS Eurovector EA-3000).
222 Nitrogen was analysed by Kjeldahl digestion (Jones and Case, 1990). The remaining
223 macronutrients (Ca, K, Mg, P, and S), micronutrients (Cu, Co, Fe, Mn, Ni and Zn) and
224 non-essential trace elements (Ba, Cd, Pb) were extracted by wet oxidation with
225 concentrated HNO₃ under pressure in a microwave digester. Macronutrients (except N)
226 were analysed by ICP-OES. Micronutrients and trace elements were analysed by
227 inductively coupled plasma mass spectroscopy (ICP-MS; Perkin Elmer, Sciex-Elan

228 5000, Cambridgeshire, UK) using the methods proposed by Jones and Case (1990).
229 Several plant reference materials were analysed to assess the quality of the analysis:
230 NCS DC 73350 (white poplar leaves, China National Analysis Centre for Iron and
231 Steel) and BCR-62 (olive tree leaves, European Community Bureau of Reference).
232 Isotopic analyses of C and N in the samples were performed using a continuous flow
233 elemental analyzer-isotopic ratio mass spectrometer (EA Thermo 1112-IRMS Thermo
234 Delta V Advantage). The precision for both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses was
235 approximately 0.2 per mil.

236

237 Community-level leaf traits and environmental heterogeneity

238

239 To study the variation in leaf functional traits at the community level, we calculated
240 community-weighted means traits. For this purpose, we selected 57 plots (3 x 3 m)
241 within the same forest site, which included most of the 32 plots where the plant species
242 were collected for leaf trait measurements (see above). The environmental conditions of
243 each of these 57 plots was previously characterised in a parallel study focused on
244 seedling growth (Pérez-Ramos et al. 2010). Canopy density was quantified by
245 hemispherical photography and image analysis (Hemiview canopy analysis software
246 ver. 2.1) and represented by the total leaf area index (LAI) and the level of light
247 intercepted by the canopy (estimated as the global site factor, GSF). Photographs were
248 taken at 0.5 m from the ground, using a horizontally-levelled digital camera and aimed
249 at the zenith, using a fish-eye lens of 180° field of view. Soil volumetric water content
250 (12 cm depth) was measured using a time-domain reflectometer (TDR, Campbell
251 Scientific Inc., Logan, UT, USA) at every season during a year. Soil samples were taken

252 for each plot at a depth of 0-25 cm and were analysed for macronutrients and
253 micronutrients (see methods above).

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

259 The relative abundance of the woody plant species was visually estimated, by
260 agreement between two experienced observers, as the percentage of plant cover in each
261 3×3 m plot. Separate 5%-increment cover estimates were given for each species in the
262 shrub (up to 3-4 m height), liana and tree layers. The relative abundance for each
263 species was then calculated by dividing its specific cover estimate by the (all-layers
264 pooled) total woody cover. Although the cover of herbaceous species also accounted for
265 the total plant cover measure in each plot (representing, on average, a 30 % all the total
266 plant cover), in this work we focused only on woody plants, and thus we rescaled the
267 woody plant cover to 100%. A total of 21 woody species were found across the 57
268 sampling sites, including the 17 species in our data set. Those four species not included
269 in our data set can be considered as rare species, as they were, on average, only present
270 in 4 out of the 57 plots.

271 Community-weighted-means (CWM) were calculated for every leaf trait as $\sum P_i$
272 $\times \text{Trait}_i$ where P_i is the relative abundance of the species “i” in the community, and
273 Trait_i is the average trait value obtained for this species “i” (Violle et al. 2007). The
274 CWM values integrate the information on community structure (local abundances of
275 species) as well as on the functional identity of the dominant species. We have selected

276 LMA_{CWM} and LDMC_{CWM} as the key functional variables which better explain the
277 response of the community to environmental factors (Garnier et al. 2001).

278

279 Data analysis

280

281 A principal components analysis (PCA) of 20 leaf traits considered in this study (2
282 morphological, 16 chemical, and 2 isotopic signatures) and 17 woody species (mean
283 values of 5 individuals for each) was performed to better understand the multivariate
284 patterns present in the data. Leaf thickness was excluded from the dataset for the
285 multivariate analysis because measurements could not be obtained for some species
286 with small-sized leaves. For comparison, a PCA analysis was also performed at the
287 community level with the CWM values of 12 leaf traits (LMA, LDMC, isotopic
288 signatures and macronutrient concentrations) for the 57 plots.

289 The bivariate relationships between species morphological traits (LMA and LDMC)
290 and the nutritional and isotopic traits, previously averaged and log-transformed, were
291 explored using standardised major axis slopes (SMAs, also known as reduced major
292 axis slopes), a statistical tool highly recommended for allometric studies (Warton et al.
293 2006). SMA slopes are fitted by minimising the sums of squares of errors in X and Y
294 dimensions simultaneously, and they show the proportional relationships between
295 variables, i.e., how one variable scales against another. SMA regressions were
296 performed using SMATR software ver. 2.0 (Falster et al. 2006). SMA fitting was also
297 applied to explore the relationships between the same traits at the community level,
298 considering the CWM at each sampling unit. The slope of the SMA regressions is of
299 special interest, since it indicates the magnitude of the scaling between the variables.

300 We only emphasized in the results section those relationships with an absolute value of
301 the SMA slope higher than one.

302 We analysed the variation in CWMs of leaf traits in response to key environmental
303 factors (bivariate relationships), by means of Pearson correlation analyses. Specifically,
304 we used light availability (GSF), soil water (annual average) and an integrated variable
305 of nutrient availability, represented by a PCA factor covering soil organic matter, and
306 the concentrations of NH_4^+ , available P and available Mg (Table 2; scores of factor 2
307 were inversely transformed for clarity).

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

311

312 **Results**

313 Leaf trait variability among species

314

315 Across the studied species, there was a strong variability in the leaf traits; for example
316 leaf mass per area varied twofold, from 60 g m^{-2} (*Rubus ulmifolius*) to 151 g m^{-2} (*Teline*
317 *linifolia*) (Table 3). In general, micronutrients and non-essential elements exhibited a
318 greater inter-specific variability than macronutrients; while among isotopic signatures,
319 $\delta^{15}\text{N}$ was more variable than $\delta^{13}\text{C}$ (Tables S2, S3 and S4). The N isotopic composition
320 was associated with the type of symbiotic/parasitic relationships of each species. Thus,
321 N-fixing species (legumes) and the hemiparasitic species (*O. alba*) exhibited positive
322 values of $\delta^{15}\text{N}$, whereas the rest of species, which had different mycorrhizal
323 associations, showed negative $\delta^{15}\text{N}$ values (Figure S1; mycorrhizal types according to
324 Maremmani et al. 2003).

325 In the multivariate analysis of leaf traits (by PCA), the first axis (explaining a
326 26.2 % of the variance) was positively related to LMA, LDMC, C, the C:N ratio and
327 $\delta^{13}\text{C}$, and negatively related to the leaf concentrations of all macronutrients (with the
328 exception of P) and micronutrients (Fig. 1). The second PCA axis was most strongly
329 correlated with the N-related variables, including N:P and $\delta^{15}\text{N}$, as well as the leaf Mn
330 and Ni concentrations. Winter deciduous species (such as *C. monogyna*) and legume
331 species (*C. villosa* and *T. linifolia*) were located towards the nutrient-rich (negative) end
332 of axis 1, in contrast to species with higher $\delta^{13}\text{C}$ and LMA values (higher than 100 g m^{-2}),
333 such as *Q. suber*, *P. lentiscus* and *P. latifolia*, which were located in the positive end.
334 Symbiotically nitrogen fixing (legume) species, in particular *C. villosa*, were separated
335 at the negative end of axis 2 (Fig. 1). For this PCA analysis, samples of *O. alba*
336 (hemiparasitic shrub) were excluded because their high concentration of P, Ca, Mg and
337 S distorted the analysis (as found in a preliminary PCA, not shown).

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

341

342 Links among leaf traits at the species and the community level

343

344 The relationships among leaf traits were not always consistent at the species and at the
345 community level. In most cases, the relationships at the community were stronger than
346 at the species level. For example, LMA and LDMC were positively and significantly
347 related when community-weighted-means were considered, whereas no significant
348 relationship was found in the cross-species analysis (Fig. 2). Interestingly, the
349 relationship between LMA and the isotopic signature of ^{13}C was positive and consistent

350 at both levels, whereas for ^{15}N the relationship was non-significant at any level (Fig. 3).
351 The high values of the SMA slope for $\delta^{13}\text{C}$ (above 4 at the species level) indicated that
352 higher LMA species were related with exponential increase in $\delta^{13}\text{C}$ and, thus, they were
353 exponentially more efficient in their use of water than lower LMA species.

354 At the species level, LMA was not significantly related with N, P or any other
355 nutrient, with the exception of Mg (Fig. 4 and Table S5). However, at the community
356 level, LMA_{CWM} was negatively related with N, Ca and Mg concentrations with a SMA
357 slope steeper than -1, indicating a proportionally higher increase of nutrient
358 concentration towards the low LMA end of the trait relationship (Fig. 4 and Table S5).

359 Bivariate relationships between LDMC and the nutrient variables followed the
360 same pattern as with LMA. In general, very few significant relationships were found
361 when species values were considered (only for Mg and Cu), while many of these
362 relationships were significant when community-weighted values were used
363 (Supplementary Material, Table S6).

364

365 Community-weighted means of leaf traits and environmental factors

366

367 There was a great variation in the plant cover (represented by the total leaf area index,
368 LAI) across the 57 sampled plots and, consequently, in the level of light intercepted by
369 the canopy (estimated as the global site factor, GSF), which could be associated to a
370 differential distribution of woody plant species (Figure S2). The explored gradient of
371 plant cover ranged from open shrublands (with $\text{LAI} < 0.5 \text{ m}^2 \text{ leaf per m}^2 \text{ soil}$)
372 dominated by small-leaved species such as *C. villosa* (72% of cover) or *E. arborea*
373 (17%), to dense forests (LAI of $2\text{-}3 \text{ m}^2 \text{ m}^{-2}$) with an overstorey of *Q. suber* (14-23%)

374 and *Q. canariensis* (11-17%) and a dense understorey of arborescent species such as *P.*
375 *lentiscus* (25-35%), *P. latifolia* (8-16%) and *E. arborea* (5-17 %).

376 The bivariate correlational analysis between the environmental factors and the
377 studied leaf traits showed that light was the factor with the highest influence on the
378 community-weighted-mean traits (Table 4). Unexpectedly, light availability was
379 negatively related with both LMA_{CWM} and $LDMC_{CWM}$ (Fig. 5), as well as with $C:N_{CWM}$
380 and $\delta^{13}C_{CWM}$. In contrast, light was positively correlated with both N_{CWM} and $\delta^{15}N_{CWM}$.
381 Soil moisture was only negatively related to C_{CWM} and $\delta^{13}C_{CWM}$, with no influence on
382 LMA_{CWM} or $LDMC_{CWM}$. Soil fertility (represented by a PCA factor, which integrates
383 soil organic matter, and the availability of NH_4^+ , P and Mg, Table 2), was weakly
384 related to the morphological traits (only a marginal positive relationship with
385 $LDMC_{CWM}$), but more closely linked to some chemical traits, such as N_{CWM} , $C:N_{CWM}$
386 and $\delta^{15}N_{CWM}$ (Table 4). In general, when the average trait values for the species pool at
387 each plot (without weighting by their relative abundance) were used the links between
388 LMA, LDMC and the environmental variables were similar (Fig 5), although the
389 explanatory power of the relationships was higher for the CWM-values.

390

391 **Discussion**

392

393 **Links among functional leaf traits at the species and community levels**

394

395 *Are LMA and LDMC related to plant nutrient economy?*

396

397 Mediterranean ecosystems provide excellent sites where exploring the relationships
398 among functional traits. The small-scale heterogeneity in the conditions of irradiance

399 and the usual concurrence of water and nutrient limitations in these systems may
400 promote the coexistence of different species with a wide range of LMA values (Poorter
401 et al. 2009). In the studied forest, LMA values ranged from 64 to 151 g m⁻², which is the
402 common range for Mediterranean woody plant species (Galmés et al. 2007; Hernández
403 et al. 2010; Mediavilla et al. 2008; Paula and Pausas 2006; Villar and Merino 2001).
404 Chemical traits were especially variable, including the isotopic signatures; nitrogen
405 isotopic signature differed among functional groups of symbiotic interactions and, thus,
406 could be used as a possible marker for mycorrhizal habit (Högberg 1990).

407 All these chemical and morphological traits showed a strong multivariate
408 covariation, especially at the community level, which can be used to characterize
409 different plant functional groups. The main variation trend was associated with the
410 acquisition-conservation trade-off (Díaz et al. 2004) and confirmed the role of LMA and
411 LDMC as indicators of differential functional strategies. Thus, communities with a
412 predominant conservative strategy exhibited high values of LMA and LDMC, positively
413 associated to C concentration, C:N ratio (sclerophyllous type) and high water use
414 efficiency (high $\delta^{13}\text{C}$ values). On the contrary, communities with a predominant
415 resource-acquisition strategy showed a lower water-use efficiency (low $\delta^{13}\text{C}$) and low
416 LMA and LDMC (Poorter and Garnier 1999; Wright and Westoby 2001).

417 The bivariate analyses confirmed that the links between the leaf morphological
418 and the leaf nutritional traits are much weaker at the species than at the community
419 level. Thus, our first hypothesis was not supported for the species pool (species mean
420 values), but it was when considering the relative abundance of the dominant species
421 constituting the community (community-weighted-means).

422 At the species level, LMA or LDMC were not related to almost any nutrient
423 concentration, not even to those elements included in the nucleic acid-protein set (N, P,

424 Cu, S, Fe, Garten 1978). These results contrast with the consistently negative
425 relationship between LMA and both N and P concentrations that has been reported for
426 global datasets (Liu et al. 2010; Ordoñez et al. 2009; Wright et al. 2004a, 2005), and
427 thus, indicates that global patterns may not hold at some local scales.

428 While trait relationships can be considered very general, they are not necessarily
429 universal (Wright et al. 2005). The specific environmental conditions in each site may
430 play a central role in the strength of the leaf morphology vs. nutrient relationships.
431 Recent analyses by Freschet et al. (2011) have shown that as much as a 50 % of the
432 global variability in SLA and leaf N occurs within communities, which may be caused
433 by large differences in the nature and strength of abiotic and biotic drivers of dominant
434 species assembly at local scales. Within the worldwide LMA spectrum, Mediterranean
435 species have low SLA (and therefore high LMA), and comparatively high N
436 concentrations (Freschet et al., 2011), which is known to enhance water conservation
437 during photosynthesis in species from low-rainfall sites (Wright et al. 2002). In some P-
438 limited ecosystems, as the studied forest, leaf morphology and N concentrations are
439 usually unrelated, and LMA and net photosynthetic capacity may be more closely
440 linked to P (Niinemets and Kull 2003; Liu et al, 2010, Chen et al., 2011). In this study,
441 however, we did not find significant links between LMA and leaf phosphorous at the
442 species or at the community level.

443 If the strength of the links between LMA and leaf nutrients depends on the
444 relative availability of the most limiting element (Niinemets and Kull 2003), then we
445 could conclude that Mg is the most limiting nutrient in the studied system, given the
446 consistent negative relationship between Mg and LMA at both levels of analysis.
447 Among the studied species, leaf Mg ranged from 1.3 to 5.1 g kg⁻¹, with a coefficient of
448 variation higher than 50 % (Table S2) probably reflecting large among-species

449 differences in the requirements for this essential element. The links between LMA and
450 leaf Mg (which is a structural component of the chlorophylls and essential for
451 photosynthesis) remain largely untested both at the local and at the global scales (but
452 see Fyllas et al. 2009).

453 Potassium was neither related to LMA. In the leaf, this element has a less
454 structural function than N or Mg, as is mainly found as a dissolved ion, contributing to
455 the leaf osmotic regulation and to the activation of many photosynthetic enzymes.
456 Despite in some local studies leaf K is significantly linked to LMA (Niinemets and Kull
457 2003; Fyllas et al., 2009), global data sets have shown that this element is very weakly
458 related to LMA, in comparison to N and P (Wright et al. 2005).

459 The range of growth forms and trait variation in this study may also explain the
460 discrepancies with the global patterns for the LMA vs. nutrient relationships. We
461 focused here on woody plant species, which have a much greater proportion of biomass
462 in non-productive tissues than herbaceous plants. The partitioning of nutrients among
463 the different plant tissues at the whole-plant level may mask the nutrient-LMA
464 relationships for a set of woody plants, in comparison to broader data sets including
465 different growth forms. To detect broad trait relationships among species, the range of
466 trait variability must be large, at least of one order of magnitude (Wright et al. 2004b).
467 Based in this data set it can be concluded that, within the normal range of LMA values
468 for Mediterranean woody plants, and despite N and P values ranged 2.6 and 3.8-fold,
469 respectively, the links between LMA and N or P among species are weak.

470 Interestingly, N and P were partly uncoupled at both levels of analysis, located
471 in opposite positions in the PCA-axes, contrasting to the global trend of positive
472 correlation between these two nutrients (Wright et al. 2004a). Again, local data set may
473 not support the global general relationships between traits (Wright et al. 2005). This

474 uncoupling may be driven by the plant-microbial interactions, which are especially
475 relevant in these nutrient-poor soils. Phosphorous availability is very low in comparison
476 to N availability, as revealed by the general high N:P ratios in the leaves (> 20) of the
477 studied plants. In these situations, the type of mycorrhizal interaction may play a central
478 role in the community assembly. For example, Pekin et al. (2011) have shown that, in
479 some Mediterranean forest ecosystems, the distribution of root traits (including the type
480 of symbiotic interactions) is driven by the N to P availability ratio in the soil.
481 Ectomycorrhizal, non-mycorrhizal and ericoid mycorrhizal species have a competitive
482 advantage over arbuscular species at sites with low N fertility where P is not limiting.
483 According to our data, N-fixation, which promotes a high N leaf concentration, does not
484 seem to promote also a high P-uptake in the studied species. Actually, plants with
485 higher P leaf concentrations tended to have lower $\delta^{15}\text{N}$, which characterized arbuscular
486 and ectomycorrhizal associations.

487 Despite that leaf ^{15}N discriminated among mycorrhizal groups, the hypothesis
488 that plant species with low LMA (and presumably a resource-acquisition strategy) have
489 a low dependence on mycorrhizal interactions for N-uptake (i.e., higher leaf ^{15}N values)
490 was not supported by our data. In contrast, the hypothesis expecting a positive
491 relationship between LMA and $\delta^{13}\text{C}$ was supported at both the species and the
492 community level, in accordance with the strong association of LMA with plant water-
493 use efficiency reported in previous studies (Cunningham et al. 1999; de Bello et al.
494 2009).

495

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

497

498 The links between the morphological (LMA and LDMC) and the chemical traits were
499 stronger at the community level. By the community-weighted mean analysis the
500 environmental filters are, somehow, taken into account, since they determine how
501 species replace each other, and thus, how different the weighted averages are across the
502 studied plots. This strong correlation among traits at the community level suggests that:
503 i) those traits have parallel shifts along the environmental gradients that determine such
504 community assembly, even though these traits are independent when the individual taxa
505 are considered, and ii) the functional structure of the studied forest communities is
506 driven not only by species identity but also by their relative abundances within the
507 community. Other studies have also found differences in trait relationships depending
508 whether the species values or the community averages were used. In a Mediterranean
509 chaparral of California, Ackerly et al. (2002) obtained stronger links between leaf size
510 and specific leaf area, as well as a stronger response of the leaf traits to insolation, when
511 using weighted averages compared to the cross-species analyses. For a set of perennial
512 species from Australia, Fonseca et al. (2000) also found that some leaf traits were not
513 related across-species, but converged along gradients of rainfall and soil phosphorus.
514 Potential limiting resources may act as the environmental filters promoting the
515 convergence of traits related to acquisition/conservation of resources (Cornwell and
516 Ackerly 2010; Sonnier et al. 2010). In this study, the consistent strong links between
517 light availability (main environmental gradient) and the most important leaf traits
518 (LMA, LDMC, N and C:N) support the convergence of independently-related traits.

519

520 **LMA and LDCM relationships with environmental filters**

521

522 Which are the environmental factors that determine the convergence of the leaf traits,
523 and thus, the functional structure in the community?

524 Among the studied environmental factors, light availability at the understorey
525 had the strongest relationship with both morphological (LMA_{CWM} and $LDMC_{CWM}$) and
526 chemical traits (N, C:N, $\delta^{13}C$ and $\delta^{15}N$ community-weighted means). Interestingly, light
527 availability was negatively related with leaf LMA_{CWM} and $LDMC_{CWM}$ (Table 4),
528 contrary to our initial hypothesis. The results were similar when species averages
529 (without weighting by the relative abundance) were used, although with a lower
530 explanatory power. The contrasting plant composition in the community along the light
531 gradient determined this pattern. On one side of the gradient, woody plant species with
532 sclerophyll leaves (higher values of LMA, LDMC and C:N) and arbuscular and ericoid
533 mycorrhizae (low foliar $\delta^{15}N$) tend to form denser forests and a shadier understorey, and
534 to exclude juvenile light-demanders (Canham et al. 1994; Sack et al. 2003). On the
535 other side, open microsites are dominated by a legume shrub (*C. villosa*) with the
536 drought-avoidance strategy (de Lillis and Fontanella 1992) of summer-deciduous leaf
537 habit (lower LMA and LDMC) and symbiotic N-fixation ability (higher $\delta^{15}N$ and lower
538 C:N). This species was not present in the plots with lowest light availability within the
539 forest (Figure S2). Woody legumes tend to have a reduced shade tolerance, and are
540 rarely found (excepting in tropical forests) in closed canopy systems (Vitousek et al.
541 2002). This successful combination of traits (summer leaf fall, short leaf life-span, low
542 LMA and high leaf N concentration) characterises the dominant plant species in some
543 dry, highly exposed microsites under Mediterranean climate (Westman 1981), and
544 represents the functional strategy of several opportunistic woody Mediterranean species
545 in canopy gaps following a perturbation (Ackerly 2004). Therefore, the observed
546 reduction of LMA and LDMC with light availability is mainly driven by the presence

547 and dominance of these deciduous legume shrub species in the gaps, and may not be
548 applicable to other forest ecosystems. This pattern also suggests that, along this
549 environmental gradient, light availability filters both the presence and the dominance of
550 the species in a similar manner, that is, selecting a reduced number of species with
551 certain traits in the most exposed sites. Since light availability was the environmental
552 factor most closely related to the dominance of the different functional traits, including
553 the chemical traits, perturbations of canopy conditions (and hence in light availability)
554 may lead to changes in the LMA and LDMC of the dominant woody species, with
555 important consequences for the biogeochemical cycles of C and N, and also of Mg, Ca,
556 K and S.

557 In spite of the widely recognised importance of soil water as a main limiting
558 resource for plants in Mediterranean conditions, we did not find any significant
559 relationship between this soil factor and the LMA_{CWM} at the forest stand scale explored.
560 Thus, the results did not support our hypothesis that this factor acts as the main
561 environmental filter. This contrasts with previous studies (of grassland communities)
562 where community-weighted LMA clearly responded to soil moisture or flooding
563 gradients (Cingolani et al. 2007; Jung et al. 2010). The lack of relationships between
564 soil moisture and leaf traits may be determined by the concurrence of contrasting leaf
565 strategies in the driest end of the gradient, that is both summer deciduous (low LMA)
566 and sclerophyll evergreen (high LMA) species can coexist in the driest plots within the
567 forest. Thus, soil moisture could promote the divergence, rather than the convergence of
568 traits in the community. On the other hand, Ackerly (2004) showed that, for a range of
569 Mediterranean woody species, minimum seasonal leaf water potential (an indicator of
570 water stress) was related to wood density, vessel diameter, twig width, and leaf
571 area:sapwood area ratios, but not to leaf life span (which is closely linked to LMA).

572 Pekin et al. (2009) also found a high correlation between water availability and leaf
573 area:sapwood area ratio in Mediterranean forest ecosystems. For a complete
574 understanding of the response of this woody plant community to soil moisture further
575 investigations focused on root and wood traits are needed.

576 Despite some recent studies have shown that soil fertility may be the
577 environmental factor with the highest influence on leaf traits at the global (Ordoñez et
578 al. 2009) and at regional scales (Fyllas et al. 2009), in this forest ecosystem the soil
579 fertility had no significant influence on LMA_{CWM} of woody species. It had some
580 influence on $LDMC_{CWM}$, although the explanatory power of this relationship was very
581 low ($r^2 = 0.09$), much lower than that of the relationship between light and LDMC ($r^2 =$
582 0.61). Nutrient limitations are more likely to influence LMA through changes in the leaf
583 density (Poorter et al. 2009). Since LDMC and leaf density are highly correlated
584 (Hodgson et al. 2011) a subtle influence of soil fertility could be more likely reflected
585 on LDMC than on LMA variation. In this forest site, light and soil fertility gradients are
586 linked and opposed; thus open, disturbed sites are usually nutrient-poor while P
587 availability largely depends on the litter supplies from oak species in the shaded
588 understorey (García et al. 2006). In this situation, LMA, which is largely influenced by
589 light conditions, may discriminate better among communities than LDMC (Hodgson et
590 al. 2011). The links between soil fertility and leaf traits found in this study, although
591 weak, also reflected the contrasting plant composition along the environmental gradient.
592 Soil fertility was positively linked to LDMC, C:N and $\delta^{13}C$, and those open, less fertile
593 sites were dominated by *Calicotome villosa*, the summer-deciduous species with the
594 lowest LDMC and the highest leaf N values in the community.

595 In conclusion, our study showed that LMA and LDMC were significantly
596 related to many other chemical leaf traits (nutrient concentrations), but only when using

597 abundance-weighted values (that is, at the community level). Thus, most of the leaf
598 traits have parallel shifts along the environmental factors that determine the community
599 assembly, even if they are independent or weakly related across individual taxa. Light
600 availability was the main environmental factor determining this convergence of the
601 community leaf traits, with no apparent influence of soil moisture on leaf traits (at the
602 studied stand level) despite the importance of water in these drought-prone ecosystems.

603

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614

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877 structure, lifespan and physiology. *New Phytol* 155 403-416.

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

Species	Code	Family	Life habit	Leaf habit	Nutritional strategy*	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 pouzinii</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

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885 Arb-Shrub, arborescent shrub; ARB, arbuscular-mycorrhizal species; ECT, ectomycorrhizal species; ERI, ericodal-mycorrhizal species; HPAR,
 886 hemiparasitic species; N-FIX, nitrogen-fixing species.

887 * Mycorrhizal types according to Maremmani et al. (2003).

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

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

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896 **Table 3** Morphological leaf traits of the studied species (mean \pm SD, n=5). LMA, leaf
 897 mass per area; LDMC, leaf dry matter content; CV, coefficient of variation (sd/mean) \times
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Species	LMA (g m ⁻²)	LDMC (g g ⁻¹)	Leaf area (cm ²)	Thickness (mm)
<i>C. monogyna</i>	73 \pm 26	0.35 \pm 0.1	4.14 \pm 1.75	0.23 \pm 0.03
<i>C. salvifolius</i>	140 \pm 37	0.35 \pm 0.05	1.81 \pm 0.67	0.47 \pm 0.07
<i>C. villosa</i>	72 \pm 12	0.24 \pm 0.01	1.12 \pm 1.04	na
<i>E. arborea</i>	97 \pm 22	0.40 \pm 0.04	0.03 \pm 0.01	na
<i>E. scoparia</i>	118 \pm 28	0.40 \pm 0.06	0.03 \pm 0.01	na
<i>L. implexa</i>	92 \pm 22	0.31 \pm 0.05	9.14 \pm 1.59	0.30 \pm 0.04
<i>O. alba</i>	115 \pm 31	0.30 \pm 0.03	0.75 \pm 0.32	na
<i>P. latifolia</i>	122 \pm 29	0.46 \pm 0.04	5.55 \pm 1.20	0.26 \pm 0.04
<i>P. lentiscus</i>	103 \pm 21	0.36 \pm 0.03	14.2 \pm 3.14	0.32 \pm 0.07
<i>P. purpurea</i>	125 \pm 28	0.38 \pm 0.04	14.3 \pm 8.9	0.66 \pm 0.08
<i>Q. canariensis</i>	116 \pm 20	0.46 \pm 0.02	20.7 \pm 10.5	0.32 \pm 0.05
<i>Q. suber</i>	144 \pm 24	0.45 \pm 0.04	7.62 \pm 2.60	0.35 \pm 0.04
<i>R. pouzinii</i>	68 \pm 5	0.39 \pm 0.01	23.3 \pm 4.2	0.18 \pm 0.01
<i>R. ulmifolius</i>	60 \pm 5	0.40 \pm 0.03	43.7 \pm 9.20	0.27 \pm 0.06
<i>S. aspera</i>	86 \pm 18	0.30 \pm 0.02	27.6 \pm 5.45	0.30 \pm 0.04
<i>T. fruticans</i>	79 \pm 21	0.35 \pm 0.05	3.97 \pm 1.24	0.33 \pm 0.01
<i>T. linifolia</i>	151 \pm 44	0.42 \pm 0.16	1.20 \pm 0.22	na
Community CV (%)	34	21	119	38

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na: for these species, leaf thickness could not be obtained

903 **Table 4** Results of the bivariate correlations between community-weighted-means traits
 904 and environmental factors. Bold characters indicate significant values after controlling
 905 for the false discovery rate (significance levels are * p<0.031; ** p<0.01; *** p<0.001).
 906 LMA, leaf mass per area; LDMC, leaf dry matter content; GSF, global site factor; LAI,
 907 leaf area index
 908

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

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914 **Figure legends**

915 **Fig. 1** Ordination of leaf traits (upper left) and woody plant species (upper right) in the
916 space defined by the first and second axes of principal component analysis (PCA). See
917 species codes in Table 1. Open and filled circles correspond to evergreen and deciduous
918 species, respectively. The comparative ordination of community-weighted leaf traits for
919 57 plots is showed in the lower panel (factor 2 has been rotated for clarity). LMA, leaf
920 mass per area; LDMC, leaf dry matter content; $\delta^{13}\text{C}$, C^{13} abundance; $\delta^{15}\text{N}$, N^{15}
921 abundance; C:N, carbon and nitrogen ratio; N:P, nitrogen and phosphorus ratio; CWM,
922 community-weighted mean

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

929

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

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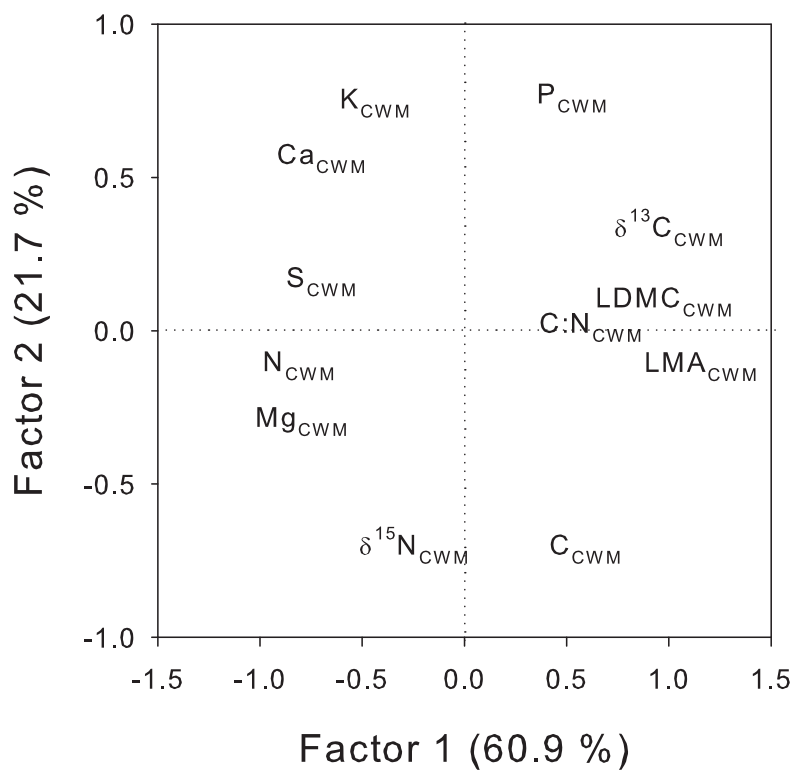
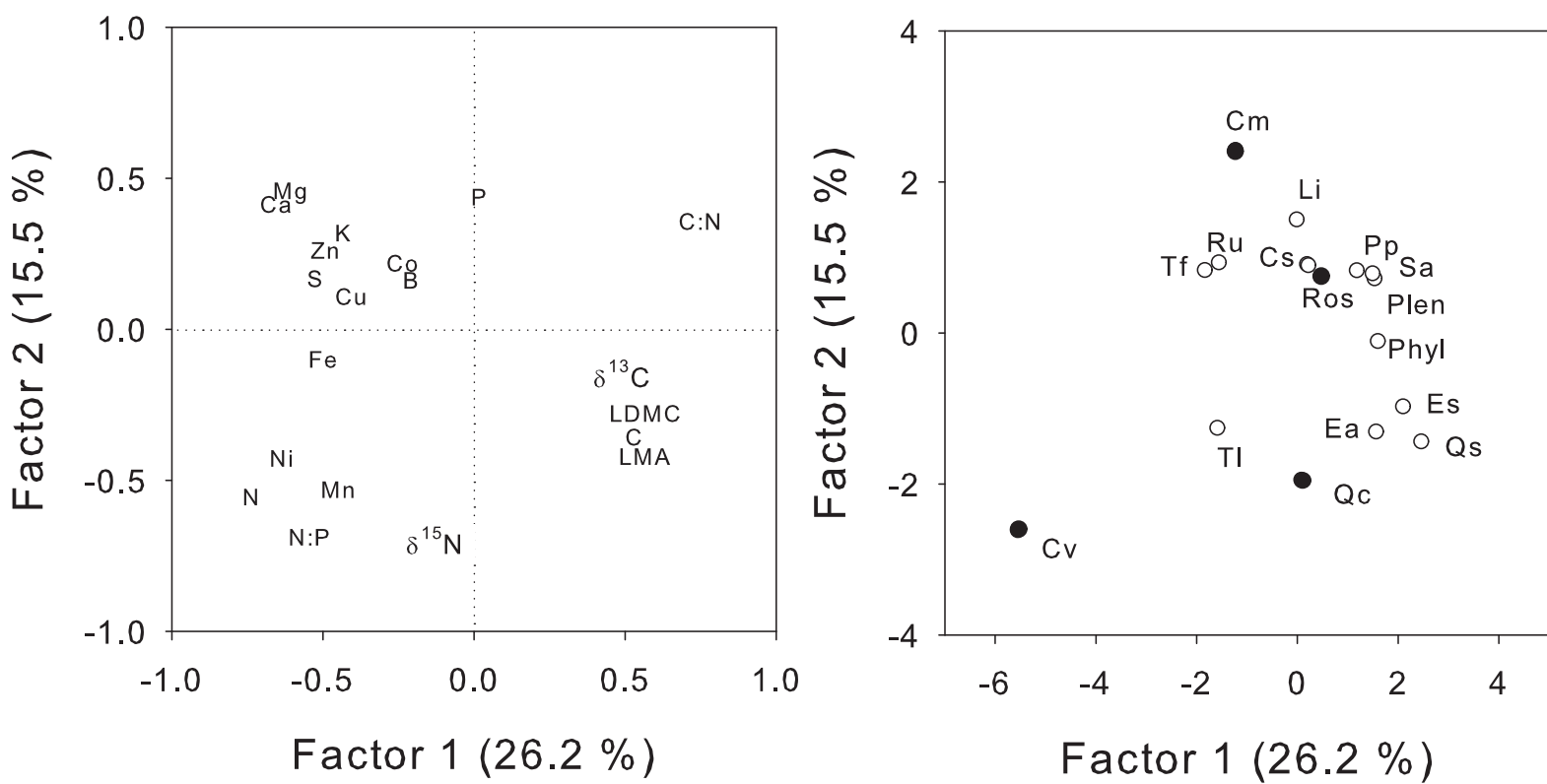
936 **Fig. 4** Bivariate relationships between leaf mass per area (LMA) and leaf nutrient
937 concentrations of N (top), Ca (centre) and Mg (bottom), at the species (left) and at the
938 community (right) level, analysed by standardised major axis (SMA) regressions. See

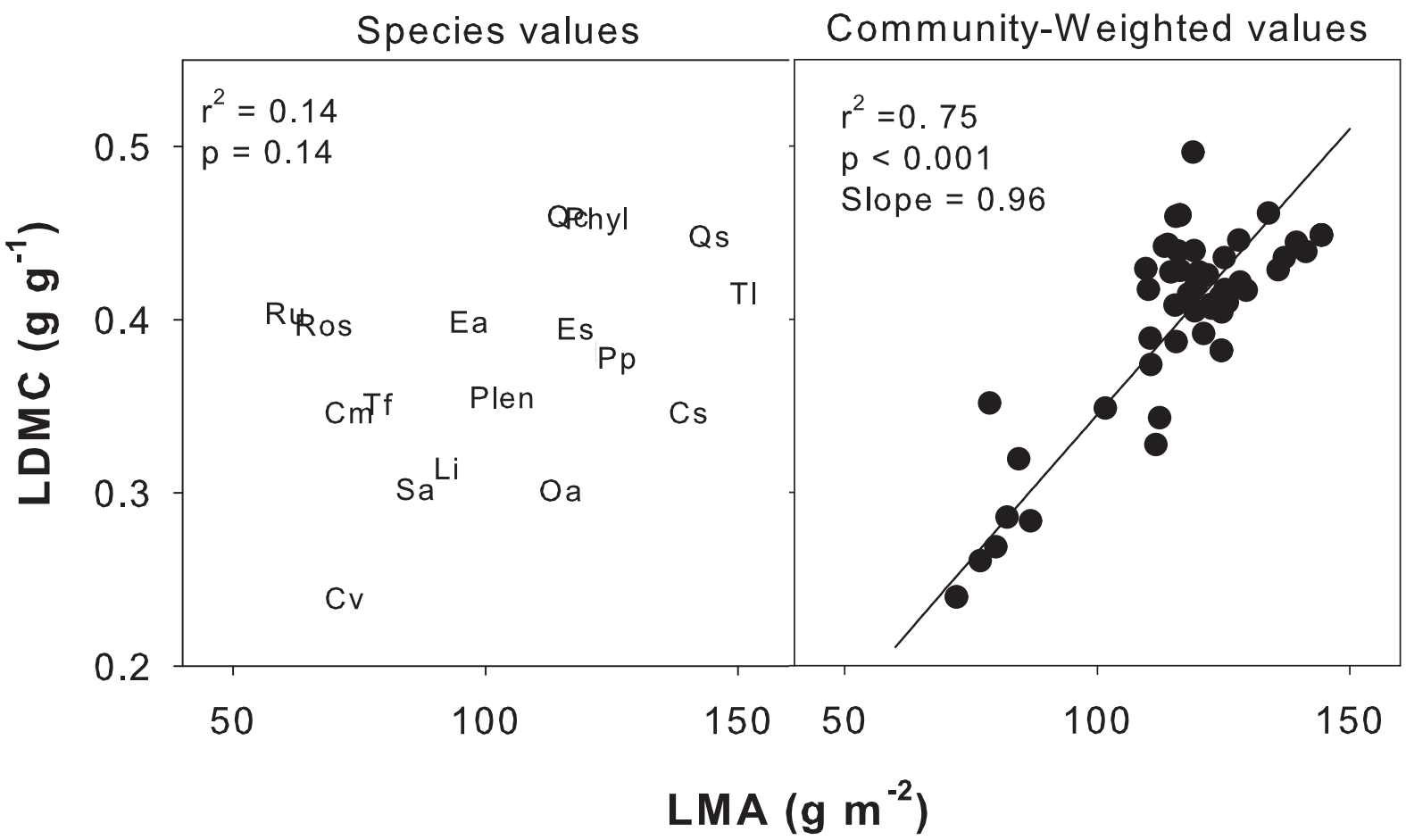
939 Table 1 for species codes. For significant correlations, the SMA slope value is also
940 indicated. See Table S5 for a complete report of the results of the bivariate correlations
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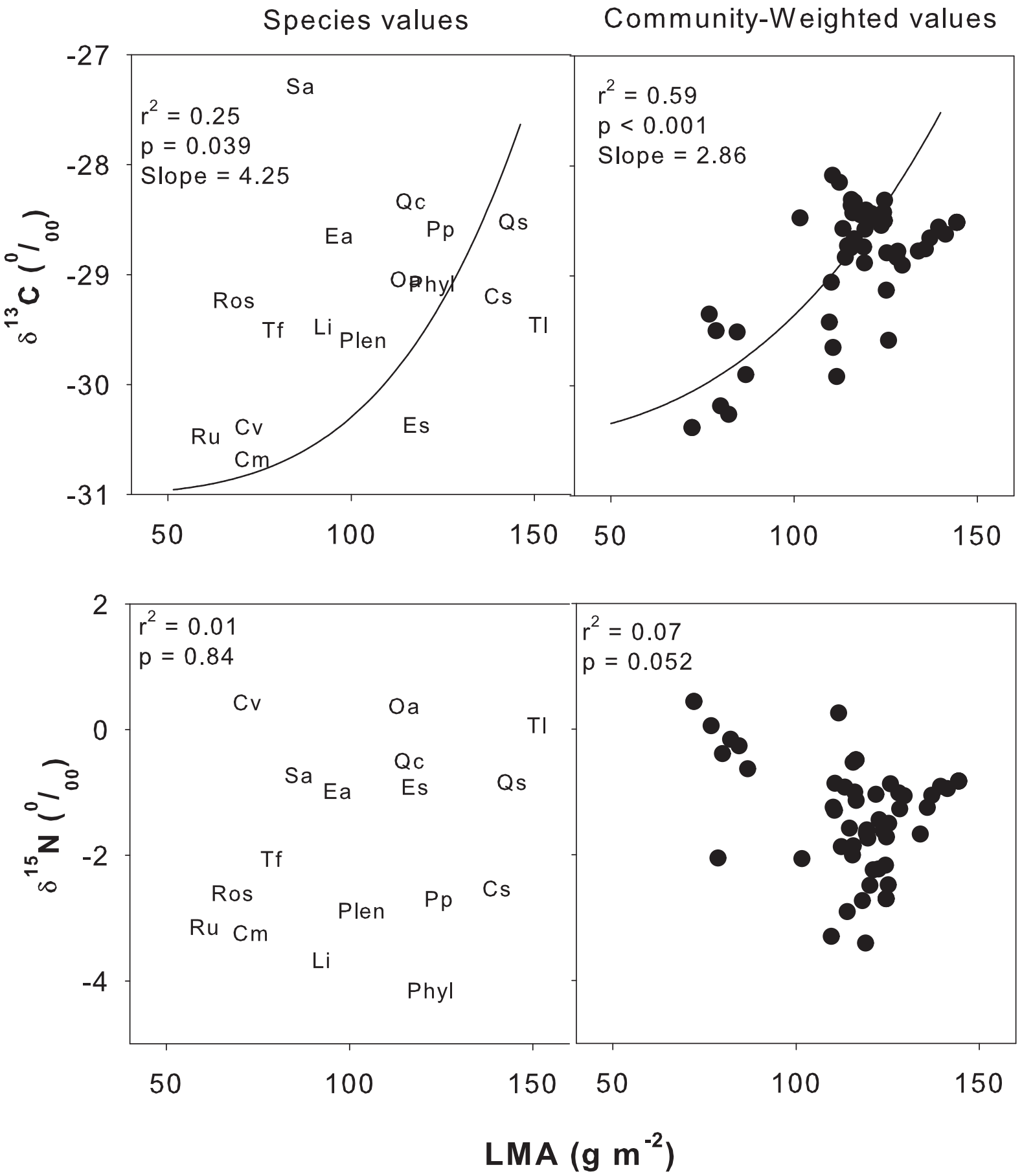
942 **Fig. 5** Relationship between main environmental gradients (light, water and soil
943 fertility) and community leaf mass per area (LMA), and leaf dry matter content
944 (LDMC). Closed circles and solid lines correspond to the community-weighted means
945 (CWM, weighting by the relative abundance of the species in the community), while
946 open triangles and dashed lines corresponds to the unweighted trait values (average of
947 present species). Light availability was estimated by global site factor (GSF), soil
948 moisture was calculated as the annual average, and soil fertility was represented by a
949 PCA factor integrating soil organic matter and the availability of NH_4^+ , P and Mg.

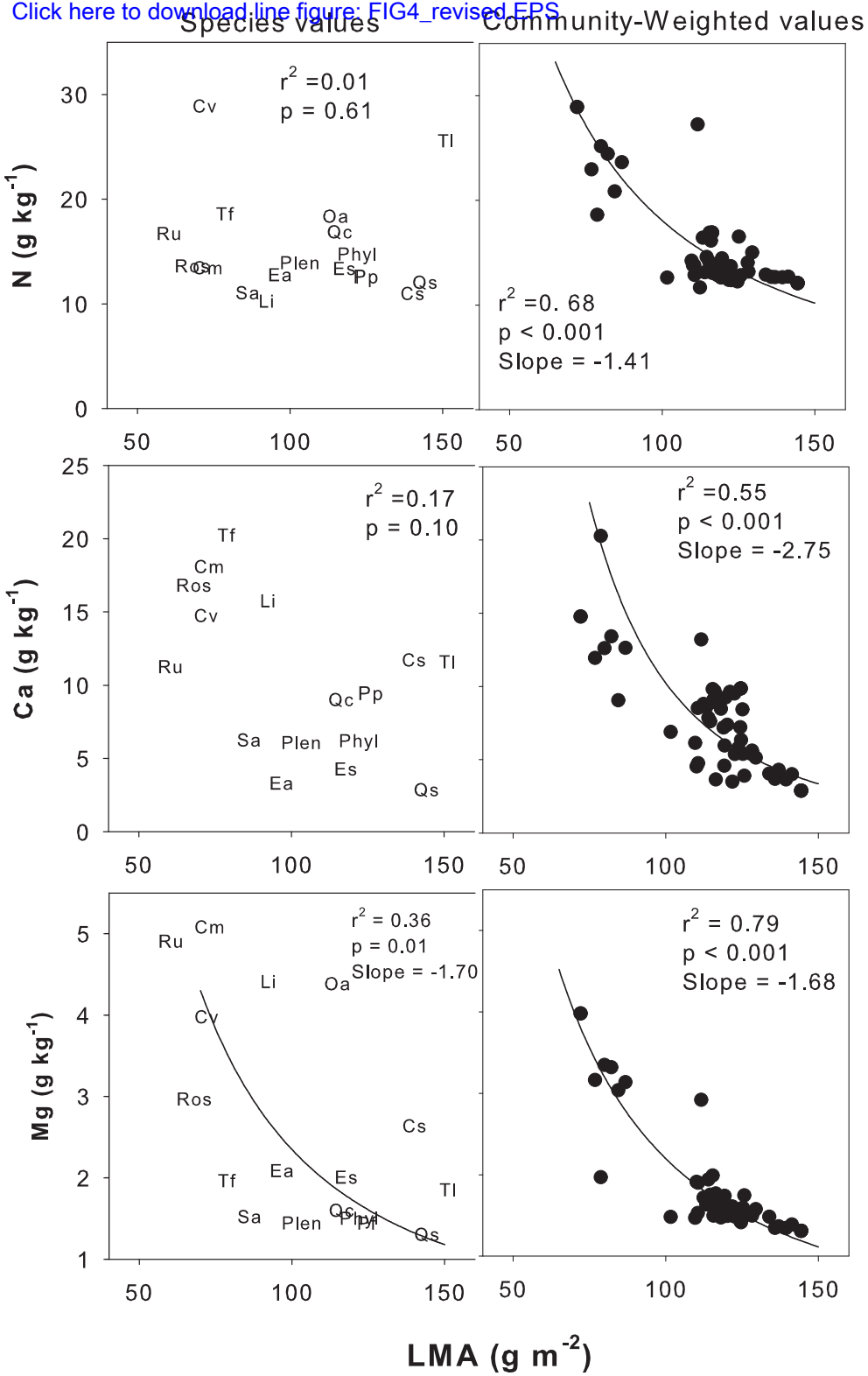
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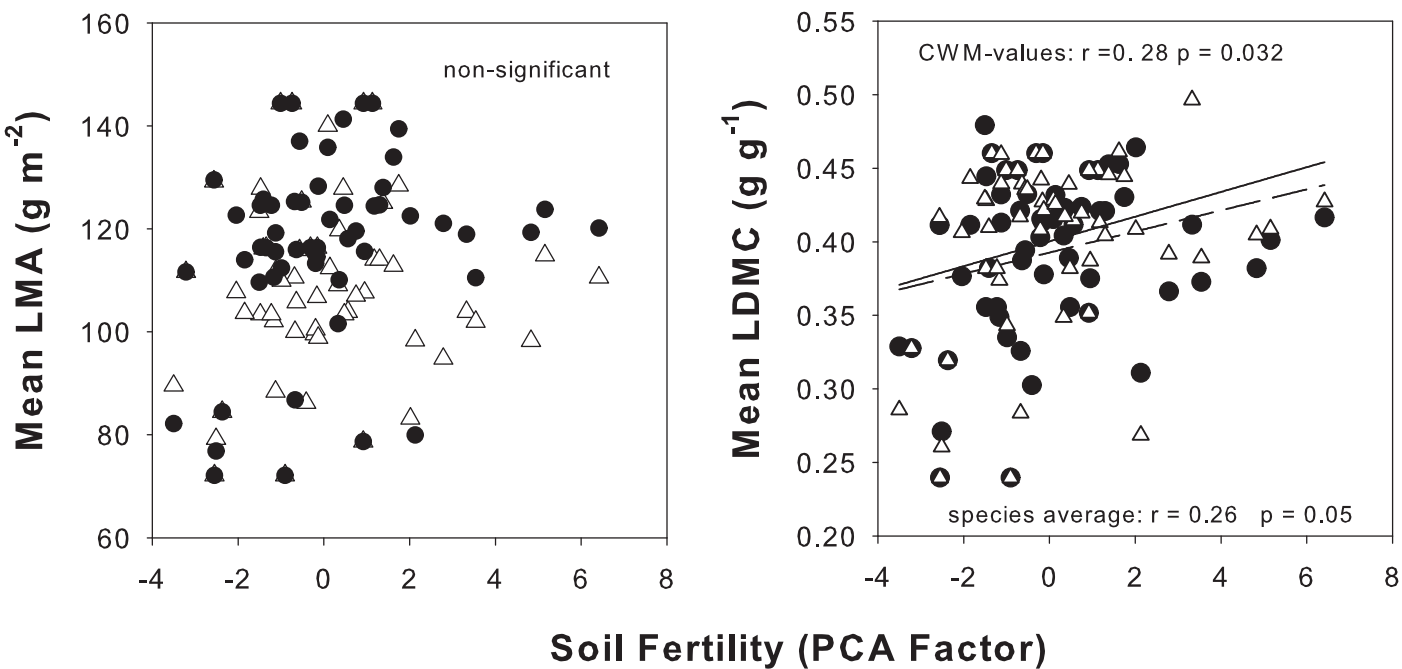
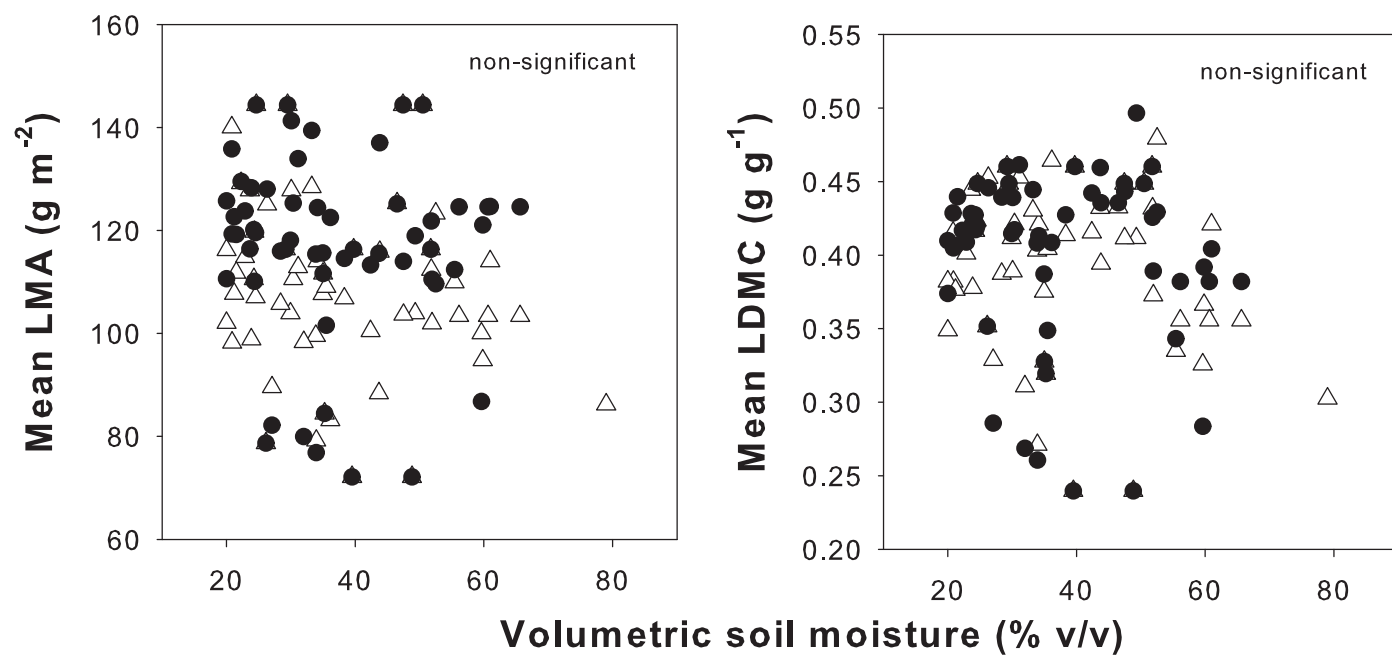
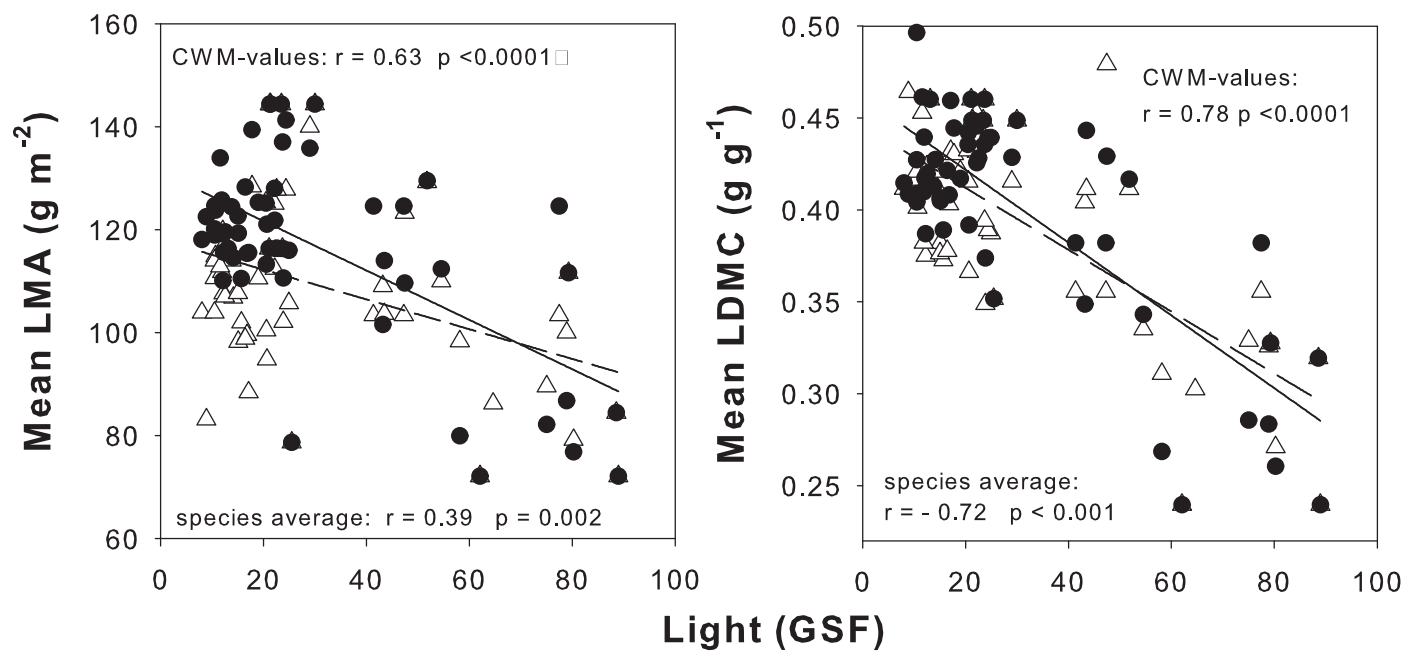
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952 **Electronic supplementary material**

953 (Submitted as separate file, for Online Publication Only)

954

955 **Table S1** Soil properties of the 32 forest plots where leaf samples were collected for
956 leaf trait analysis

957

958 **Table S2** Macronutrient concentrations in the leaves of the studied species (mean \pm SD,
959 n=5). The coefficient of variation at the community level (CV) is also indicated

960

961 **Table S3** Micronutrient and trace-element concentrations (mg kg^{-1}) in the leaves of the
962 studied species (mean \pm SD, n=5). The coefficient of variation at the community level
963 (CV) is also indicated

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965 **Table S4** Leaf isotopic signatures of ^{15}N and ^{13}C (‰) of the studied species (mean \pm
966 SD, n=5). Community range [min., max.] is also indicated

967

968 **Table S5** Summary of the SMA regression results between the leaf mass per area
969 (LMA) and the rest of studied leaf traits, at the species and the community level. For
970 those significant relationships (bold values), slope *P*-values and intercept are also
971 indicated. Those slope values with a *P*-value < 0.05 were significantly different than 1.

972

973 **Table S6** Summary of the SMA regression results between the leaf dry matter content
974 (LDMC) and the rest of studied leaf traits, at the species and the community level. For

975 those significant relationships (bold values), slope *P*-values and intercept are also
976 indicated. Those slope values with a *P*-value < 0.05 were significantly different than 1.

977

978 **Figure S1** Leaf $\delta^{15}\text{N}$ values of the different functional groups with symbiotic/parasitic
979 interactions. ECT, ectomycorrhizal species; ARB, arbuscular mycorrhizal species; ERI,
980 ericoid mycorrhizal species; N-FIX, Nitrogen-fixing species; HPAR, hemiparasitic
981 species.

982 **Figure S2** Relative abundance (% cover) of main woody species in the community
983 across different classes of canopy leaf area index.

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1 **Electronic supplementary material**

2 (for Online Publication Only)

3

4 **Table S1** Soil properties of the 32 forest plots where leaf samples were collected for
5 leaf trait analysis.

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Soil variable	Mean \pm SD	Range
pH	5.9 \pm 0.6	[4.86 - 8.3]
Organic matter (%)	9.9 \pm 2.8	[6.4 - 19.0]
Total N (%)	0.29 \pm 0.10	[0.16 - 0.55]
Available nutrients (mg kg ⁻¹)		
NH ₄ ⁺	23.9 \pm 14.2	[6.1- 68.5]
P	2.44 \pm 1.69	[0.35 - 7.54]
Ca	1781 \pm 1214	[396 - 5469]
K	126 \pm 72	[46-297]
Mg	175 \pm 79	[53 - 362]
Cu	4.17 \pm 3.68	[0.98 - 17.5]
Fe	305 \pm 171	[115 - 914]
Mn	402 \pm 243	[151 -1149]
S	3.35 \pm 0.43	[2.8 - 4.30]
Zn	5.05 \pm 4.11	[0.08 -15.86]

Table S2 Macronutrient concentrations in the leaves of the studied species (mean \pm SD, n=5). The coefficient of variation at the community level (CV) is also indicated.

Species	C (g kg ⁻¹)	N (g kg ⁻¹)	P (g kg ⁻¹)	Ca (g kg ⁻¹)	K (g kg ⁻¹)	Mg (g kg ⁻¹)	S (g kg ⁻¹)
<i>C. monogyna</i>	485 \pm 14	13.5 \pm 0.6	1.06 \pm 0.11	18.1 \pm 2.8	14.8 \pm 1.3	5.08 \pm 0.82	1.55 \pm 0.14
<i>C. salvifolius</i>	490 \pm 7	11.0 \pm 1.3	0.90 \pm 0.12	11.7 \pm 3.3	7.7 \pm 1.5	2.64 \pm 0.60	1.18 \pm 0.11
<i>C. villosa</i>	481 \pm 12	28.9 \pm 6.0	0.71 \pm 0.20	18.4 \pm 4.4	16.1 \pm 5.0	3.98 \pm 1.44	1.58 \pm 0.40
<i>E. arborea</i>	552 \pm 42	12.8 \pm 1.4	0.59 \pm 0.08	3.3 \pm 0.5	8.3 \pm 1.9	2.09 \pm 0.37	1.28 \pm 0.17
<i>E. scoparia</i>	584 \pm 16	13.4 \pm 3.1	0.67 \pm 0.17	4.3 \pm 0.6	6.6 \pm 2.6	2.01 \pm 0.42	1.49 \pm 0.32
<i>L. implexa</i>	487 \pm 11	10.3 \pm 2.3	0.65 \pm 0.15	15.8 \pm 3.7	23.1 \pm 1.9	4.41 \pm 0.52	1.51 \pm 0.44
<i>O. alba</i>	453 \pm 26	18.4 \pm 4.8	2.73 \pm 1.00	23.5 \pm 5.3	34.5 \pm 7.2	4.39 \pm 1.35	2.43 \pm 0.40
<i>P. latifolia</i>	524 \pm 10	14.8 \pm 2.1	0.95 \pm 0.21	6.2 \pm 1.5	9.5 \pm 2.1	1.51 \pm 0.45	1.36 \pm 0.32
<i>P. lentiscus</i>	515 \pm 19	13.9 \pm 1.2	1.14 \pm 0.29	6.1 \pm 2.0	12.3 \pm 2.5	1.45 \pm 0.25	1.50 \pm 0.56
<i>P. purpurea</i>	484 \pm 11	12.6 \pm 1.9	1.15 \pm 0.16	9.9 \pm 4.2	19.5 \pm 4.1	1.45 \pm 0.37	1.21 \pm 0.21
<i>Q. canariensis</i>	497 \pm 15	16.9 \pm 2.0	0.96 \pm 0.20	9.0 \pm 2.2	9.7 \pm 1.8	1.60 \pm 0.45	1.36 \pm 0.13
<i>Q. suber</i>	516 \pm 7	12.1 \pm 1.4	0.99 \pm 0.08	2.9 \pm 0.4	7.7 \pm 0.9	1.31 \pm 0.14	0.94 \pm 0.05
<i>R. pouzinii</i>	476 \pm 15	13.6 \pm 2.2	0.91 \pm 0.12	16.8 \pm 2.4	11.9 \pm 3.1	2.97 \pm 0.80	1.34 \pm 0.11
<i>R. ulmifolius</i>	487 \pm 10	16.8 \pm 2.1	1.00 \pm 0.15	11.3 \pm 1.6	13.9 \pm 1.4	4.91 \pm 0.83	1.46 \pm 0.26
<i>S. aspera</i>	517 \pm 8	11.1 \pm 1.4	1.11 \pm 0.42	6.3 \pm 2.1	15.5 \pm 5.1	1.53 \pm 0.66	1.60 \pm 0.45
<i>T. fruticans</i>	487 \pm 15	18.6 \pm 2.5	0.93 \pm 0.22	20.3 \pm 8.5	17.4 \pm 5.9	1.97 \pm 0.44	1.75 \pm 0.18
<i>T. linifolia</i>	516 \pm 3	25.6 \pm 2.1	0.79 \pm 0.07	11.6 \pm 2.9	18.8 \pm 1.2	1.86 \pm 0.24	1.53 \pm 0.15
Community CV (%)	6.7	35	54	60	52	55	27

Table S3 Micronutrient and trace-element concentrations (mg kg^{-1}) in the leaves of the studied species (mean \pm SD, $n=5$). The coefficient of variation at the community level (CV) is also indicated.

Species	B	Ba	Fe	Cd	Co	Cu	Mn	Ni	Pb	Zn
<i>C. monogyna</i>	44.4 \pm 13.7	86.9 \pm 20.7	131 \pm 44	0.144 \pm 0.323	0.263 \pm 0.254	13.9 \pm 13.2	107.7 \pm 34.3	1.51 \pm 0.31	0.60 \pm 0.84	40.0 \pm 16.2
<i>C. salvifolius</i>	51.6 \pm 8.5	32.9 \pm 15.3	171 \pm 31	0.229 \pm 0.230	1.222 \pm 1.287	8.7 \pm 7.6	202.2 \pm 195.4	3.46 \pm 1.57	0.25 \pm 0.45	70.8 \pm 40.1
<i>C. villosa</i>	42.4 \pm 25.2	15.4 \pm 12.3	184 \pm 50	0.000 \pm 0.000	0.157 \pm 0.221	55.9 \pm 43.3	543.9 \pm 160.2	7.17 \pm 3.09	1.97 \pm 2.30	58.2 \pm 36.1
<i>E. arborea</i>	46.8 \pm 16.0	17.0 \pm 4.5	133 \pm 75	0.007 \pm 0.012	0.086 \pm 0.045	17.7 \pm 9.0	105.8 \pm 50.4	2.47 \pm 0.75	0.99 \pm 0.42	21.3 \pm 5.4
<i>E. scoparia</i>	54.4 \pm 20.3	9.5 \pm 1.7	74 \pm 28	0.117 \pm 0.262	0.032 \pm 0.041	13.4 \pm 12.9	23.3 \pm 9.8	1.28 \pm 0.55	0.55 \pm 0.68	21.1 \pm 9.8
<i>L. implexa</i>	38.0 \pm 12.1	34.0 \pm 7.3	97 \pm 28	0.054 \pm 0.029	0.059 \pm 0.006	46.1 \pm 36.3	71.3 \pm 26.3	1.87 \pm 1.25	2.38 \pm 1.86	51.5 \pm 35.3
<i>O. alba</i>	37.4 \pm 22.2	40.1 \pm 25.3	58 \pm 13	0.081 \pm 0.017	0.344 \pm 0.140	23.8 \pm 7.5	927.1 \pm 319.0	8.20 \pm 2.81	0.46 \pm 0.42	37.4 \pm 16.8
<i>P. latifolia</i>	14.6 \pm 4.5	11.8 \pm 3.9	59 \pm 22	< 0.001	0.065 \pm 0.132	22.6 \pm 15.5	29.8 \pm 5.3	3.33 \pm 0.80	0.83 \pm 0.86	44.1 \pm 15.2
<i>P. lentiscus</i>	23.2 \pm 8.9	19.1 \pm 11.3	54 \pm 26	< 0.001	< 0.001	36.3 \pm 21.1	52.5 \pm 25.8	1.04 \pm 0.49	1.68 \pm 1.24	32.4 \pm 14.7
<i>P. purpurea</i>	55.6 \pm 22.4	12.3 \pm 4.4	193 \pm 44	< 0.001	0.016 \pm 0.021	11.9 \pm 5.8	63.9 \pm 20.3	1.67 \pm 1.00	0.26 \pm 0.34	21.8 \pm 5.3
<i>Q. canariensis</i>	47.0 \pm 9.9	43.0 \pm 15.9	114 \pm 11	< 0.001	0.046 \pm 0.052	17.2 \pm 6.7	643.7 \pm 203.9	3.43 \pm 0.83	0.69 \pm 0.41	25.5 \pm 7.1
<i>Q. suber</i>	25.1 \pm 2.5	7.0 \pm 2.2	77 \pm 19	< 0.001	0.111 \pm 0.119	19.2 \pm 9.7	363.0 \pm 69.2	3.42 \pm 0.94	0.73 \pm 0.61	23.5 \pm 4.7
<i>R. pouzinii</i>	61.6 \pm 14.6	23.3 \pm 12.8	100 \pm 23	0.008 \pm 0.008	0.066 \pm 0.010	13.1 \pm 5.1	121.9 \pm 50.7	1.85 \pm 0.35	0.67 \pm 0.30	19.9 \pm 3.8
<i>R. ulmifolius</i>	43.8 \pm 13.4	26.6 \pm 6.9	171 \pm 40	0.007 \pm 0.002	0.173 \pm 0.069	15.7 \pm 10.7	245.2 \pm 85.5	2.88 \pm 0.70	0.79 \pm 0.58	31.1 \pm 9.9
<i>S. aspera</i>	22.9 \pm 11.1	18.8 \pm 24.2	66 \pm 26	< 0.001	0.000 \pm 0.000	33.8 \pm 32.7	86.1 \pm 85.8	1.27 \pm 0.87	1.59 \pm 1.85	35.7 \pm 20.8
<i>T. fruticans</i>	29.5 \pm 4.0	33.2 \pm 10.6	135 \pm 17	0.070 \pm 0.052	0.162 \pm 0.088	56.7 \pm 32.0	193.5 \pm 104.1	5.13 \pm 0.75	2.73 \pm 1.74	62.5 \pm 30.7
<i>T. linifolia</i>	28.6 \pm 3.5	21.4 \pm 6.5	165 \pm 23	0.004 \pm 0.007	0.115 \pm 0.092	6.0 \pm 4.3	313.8 \pm 57.1	2.70 \pm 0.75	0.33 \pm 0.28	36.6 \pm 1.7
Community CV (%)	47	83	48	291	235	98	111	74	119	63

Table S4 Leaf isotopic signatures of ^{15}N and ^{13}C (‰) of the studied species (mean \pm SD, n=5). Community range [min., max.] is also indicated.

	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>C. monogyna</i>	-3.23 \pm 0.74	-30.7 \pm 0.9
<i>C. salvifolius</i>	-2.52 \pm 0.92	-29.2 \pm 0.9
<i>C. villosa</i>	0.44 \pm 0.72	-30.4 \pm 0.8
<i>E. arborea</i>	-0.97 \pm 1.41	-28.6 \pm 1.1
<i>E. scoparia</i>	-0.91 \pm 1.54	-30.4 \pm 1.6
<i>L. implexa</i>	-3.66 \pm 0.53	-29.5 \pm 1.6
<i>O. alba</i>	0.38 \pm 0.94	-29.0 \pm 0.2
<i>P. latifolia</i>	-4.15 \pm 0.42	-29.1 \pm 1.7
<i>P. lentiscus</i>	-2.88 \pm 0.97	-29.6 \pm 1.2
<i>P. purpurea</i>	-2.70 \pm 0.77	-28.5 \pm 1.1
<i>Q. canariensis</i>	-0.49 \pm 0.42	-28.3 \pm 0.8
<i>Q. suber</i>	-0.83 \pm 0.13	-28.5 \pm 0.5
<i>R. pouzinii</i>	-2.59 \pm 0.98	-29.2 \pm 0.5
<i>R. ulmifolius</i>	-3.14 \pm 1.14	-30.5 \pm 0.5
<i>S. aspera</i>	-0.72 \pm 0.66	-27.3 \pm 1.2
<i>T. fruticans</i>	-2.05 \pm 1.95	-29.5 \pm 1.5
<i>T. linifolia</i>	0.08 \pm 0.31	-29.5 \pm 1.1
Community range	[-4.14, 0.43]	[-30.7, -27.3]

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Table S5 Summary of the SMA regression results between the leaf mass per area (LMA) and the rest of studied leaf traits, at the species and the community level. For those significant relationships (bold values), slope *P*-values and intercept are also indicated. Those slope values with a *P*-value < 0.05 were significantly different than 1.

	Species level				Community level			
	<i>r</i> ²	<i>P</i> -value	Slope		<i>r</i> ²	<i>P</i> -value	Slope	
			Value	<i>P</i> -value			Value	<i>P</i> -value
LDMC	0.14	0.14	0.6		0.74	< 0.001	1.04	0.604
C	0.08	0.27	0.21		0.12	0.008	0.21	< 0.001
N	0.01	0.65	-1.01		0.68	< 0.001	-1.42	< 0.001
N*	0.06	0.378	-0.68					
C:N	0.03	0.49	1.07		0.61	< 0.001	1.39	< 0.001
d ¹⁵ N	0	0.84	3.86		0.07	0.052	-2.2	
d ¹³ C	0.25	0.04	4.21	< 0.001	0.59	< 0.001	2.86	< 0.001
P**	0	0.95	-0.72		0.33	< 0.001	0.81	0.059
Ca	0.17	0.1	-2.24		0.55	< 0.001	-2.75	< 0.001
K	0.05	0.39	-1.56		0.25	< 0.001	-1.68	< 0.001
Mg	0.36	0.01	-1.7	0.02	0.79	< 0.001	-1.68	< 0.001
S	0.11	0.19	-0.69		0.73	< 0.001	-0.86	0.031
Ba	0.14	0.14						
Co	0.05	0.39						
Cu	0.19	0.09						
Fe	0.03	0.51						
Mn	0.00	0.98						
Ni	0.00	0.87						
Zn	0.01	0.76						

* excluding N-fixing species from the data set

** excluding hemiparasitic species (*Osyris alba*) from the data set

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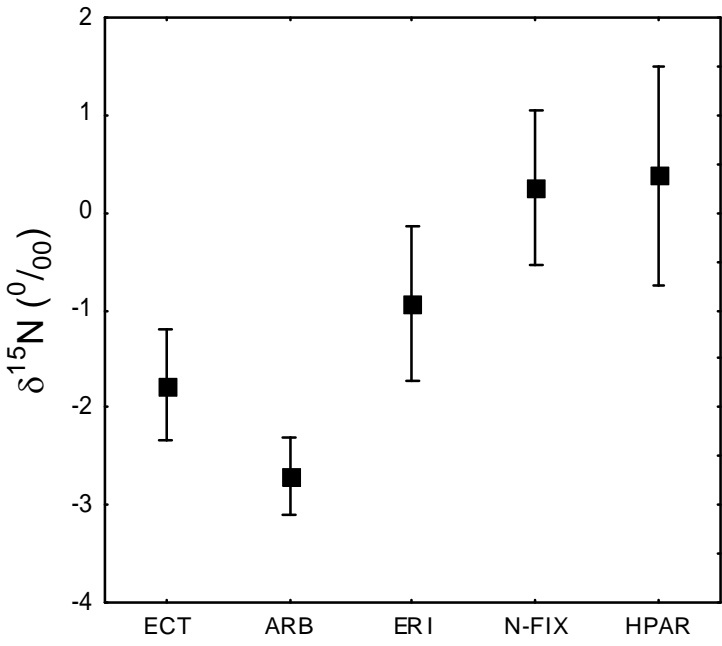
61 **Table S6** Summary of the SMA regression results between the leaf dry matter content
 62 (LDMC) and the rest of studied leaf traits, at the species and the community level. For
 63 those significant relationships (bold values), slope *P*-values and intercept are also
 64 indicated. Those slope values with a *P*-value < 0.05 were significantly different than 1.
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	Species level				Community level				
	r ²	<i>P</i> -value	Slope		r ²	<i>P</i> -value	Slope		
			Value	p value			Value	p-value	
LMA	0.14	0.14	0.60		LMA	0.74	< 0.001	1.04	0.607
C	0.18	0.09	0.35	< 0.001	C	0.16	0.002	0.22	< 0.001
N	0.04	0.46	-1.67		N	0.57	< 0.001	-1.47	< 0.001
C:N	0.07	0.33	1.77		C:N	0.50	< 0.001	1.44	< 0.001
δ ¹⁵ N	0.08	0.28	-6.38		δ ¹⁵ N	0.13	0.005	-2.28	< 0.001
δ ¹³ C	0.04	0.43	7.04		δ ¹³ C	0.65	< 0.001	2.96	< 0.001
P	0.02	0.59	-1.99		P	0.26	< 0.001	0.84	0.136
Ca	0.22	0.06	-3.70		Ca	0.36	< 0.001	-2.85	< 0.001
K	0.29	0.03	-2.58		K	0.29	< 0.001	-1.74	< 0.001
Mg	0.24	0.05	-2.81	< 0.001	Mg	0.76	< 0.001	-1.74	< 0.001
S	0.29	0.03	-1.14		S	0.39	< 0.001	-0.89	0.268
Ba	0.058	0.35							
Co	0.031	0.501							
Cu	0.308	0.021	-3.71	< 0.001					
Fe	0.008	0.738							
Mn	0.043	0.427							
Ni	0.05	0.388							
Zn	0.289	0.026	-2.36						

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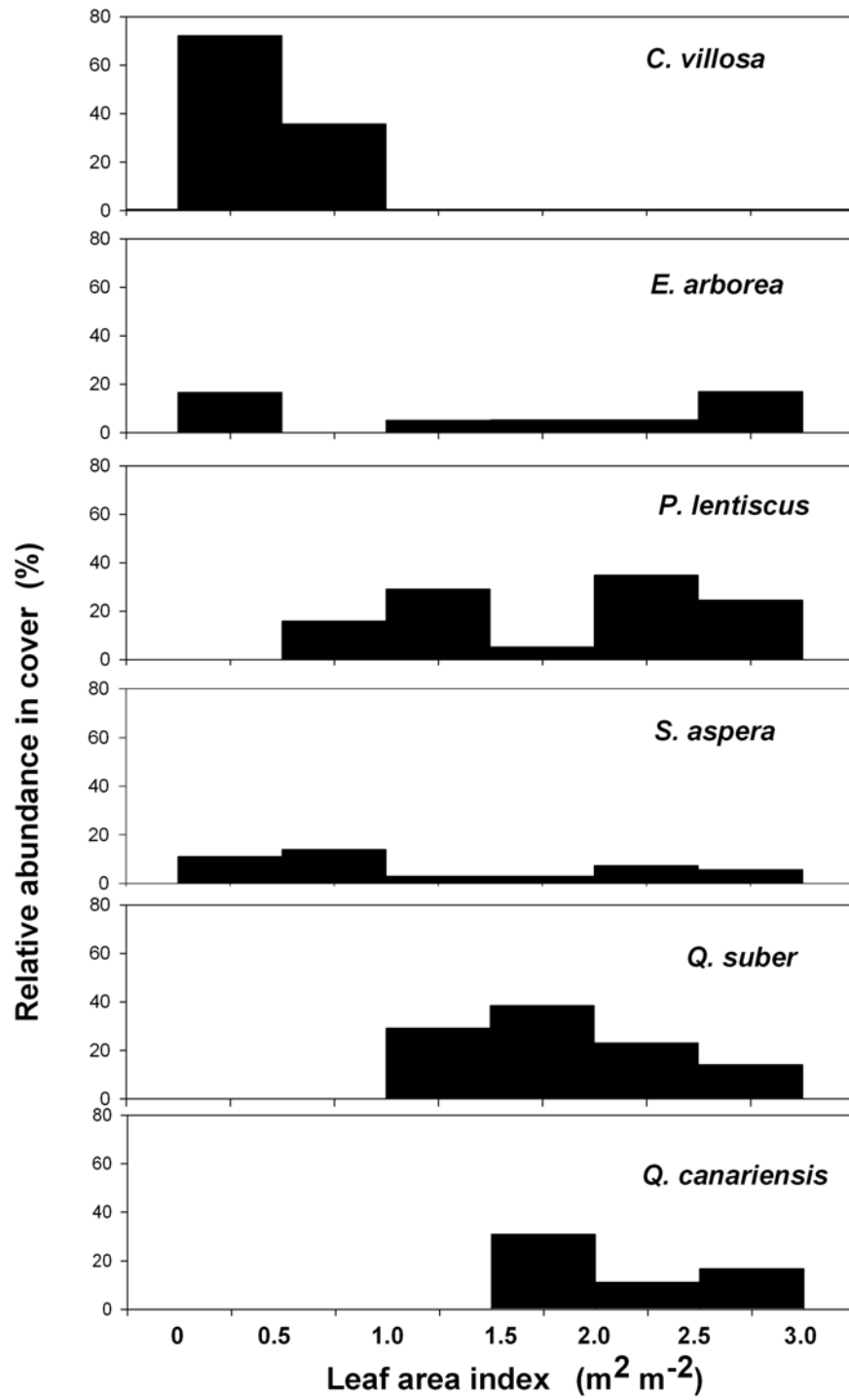
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Figure S1 Leaf $\delta^{15}\text{N}$ values of the different functional groups with symbiotic/parasitic interactions. ECT, ectomycorrhizal species; ARB, arbuscular mycorrhizal species; ERI, ericoid mycorrhizal species; N-FIX, Nitrogen-fixing species; HPAR, hemiparasitic species.



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Figure S2 Relative abundance (% cover) of main woody species in the community across different classes of canopy leaf area index.



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