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

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Abstract

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

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

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

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

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

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

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Introduction

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

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

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

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

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

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

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

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

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

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

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

Material and Methods

Study area, species selection and sampling design

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

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

They were also selected to cover the widest variability of leaf traits in the area. Nomenclature follows Valdés et al. (1987), with exception of *Teline linifolia* (Talavera and Gibbs, 1999). In late spring 2008, during the peak of vegetative growth, 32 plots (3×3m) 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

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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 laminae 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

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 x 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 the relative abundance of the species “i” in the community, and Trait_i is the average trait value obtained for this species “i” (Violle et al. 2007). The CWM values integrate the information on community structure (local abundances of species) as well as on the functional identity of the dominant species. We have selected

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

Data analysis

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

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

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

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

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

Results

Leaf trait variability among species

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

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

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

Links among leaf traits at the species and the community level

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

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

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

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

Community-weighted means of leaf traits and environmental factors

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

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

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

Discussion

Links among functional leaf traits at the species and community levels

Are LMA and LDMC related to plant nutrient economy?

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

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

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

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

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

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

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

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

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

LMA and LDCM relationships with environmental filters

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

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

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

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

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

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

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

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

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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).

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.

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

Table 3 Morphological leaf traits of the studied species (mean $\pm$ SD, n=5). LMA, leaf mass per area; LDMC, leaf dry matter content; CV, coefficient of variation (sd/mean) $\times$ 100

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

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

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

	LMA _{CWM}	LDMC _{CWM}	C _{CWM}	N _{CWM}	C:N _{CWM}	$\delta^{13}\text{C}_{\text{CWM}}$	$\delta^{15}\text{N}_{\text{CWM}}$
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

Figure legends

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

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

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

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 unweighted 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.

Electronic supplementary material

(Submitted as separate file, for Online Publication Only)

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

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

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

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

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.

Table S6 Summary of the SMA regression results between the leaf dry matter content (LDMC) 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.

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.

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

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