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# Climate and taxonomy underlie different elemental concentrations and stoichiometries of forest species: the optimum "biogeochemical niche".

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**Abstract** We previously hypothesised the existence of a "biogeochemical niche" occupied by each plant species. Different species should have a specific elemental composition, stoichiometry and allocation as a consequence of their particular metabolism, physiology and structure (morphology) linked to their optimal functioning under the environmental (abiotic and biotic) conditions where they have evolved. We tested this hypothesis using data from the Catalan Forestry Inventory that covers different forest groups growing under a large climatic gradient. Mediterranean species that occupy hotter-drier environments have lower leaf N, P and K concentrations than non-Mediterranean forest species. Within a determined climatic biome, different species competing in the same space have different elemental compositions and allocations linked to their taxonomical differences and their phenotypic plasticity. Gymnosperms have a proportionally higher elemental allocation to leaves than to wood, higher C concentrations, and lower N, P and K concentrations mainly in the stem and branches than angiosperms. The differences among species are linked to asymmetrical use of different elements, suggesting that the biogeochemical niche is a final expression and consequence of long-term species adaptation to particular abiotic factors, ecological role (stress tolerant, ruderal, competitor), different soil occupation and use of resources to avoid interspecific competition, and finally of a certain degree of flexibility to adapt to current environmental shifts.

**Keywords** Biogeochemical niche; C:N; Mediterranean; N:P; Nutrients; Phosphorus; Potassium

## Introduction

Several studies have found strong relationships of climate and soil type gradients with the N:P ratio of terrestrial plants (Reich and Oleksyn 2004; Kerkhoff et al. 2005; Zheng and Shangguan 2007; Yuan and Chen 2009; Vitousek et al. 2010; Sardans et al. 2011a; Sardans and Peñuelas 2013) suggesting that terrestrial plant species should have an optimum N:P ratio enabling them to better adapt to their optimum abiotic niche (Sardans et al. 2012a). Moreover, apart from N and P, other elements such as K can be also limiting in terrestrial plant communities. Evidence of K limitation has been observed from temperate (Tripler et al. 2006) to tropical ecosystems (Tripler et al. 2006; Wright et al. 2011; Baribaut et al. 2012; Santiago et al. 2012). Although less than N, P and K, other nutrients such as S, Mg or Ca also become limiting in terrestrial plant communities (Hailes et al. 1997; Naples and Fisk 2010; Baribault et al. 2012; Lapeins et al. 2013). Thus a better understanding of variations in all essential plant nutrients and their critical relationships (rather than in N and P centric perspective) is essential in holistic bigeochemical models. Han et al. (2011) by analyzing 11 different nutrients in 1900 plant species across China observed that all these elements were different in relation to climate, soil and functional type, showing the need of the use of most nutrients as possible to reach a more holistic approach to ecological plant nutrition knowledge and for the development of multiple elements biogeochemical models.

The study of the causes and factors that can help to understand niche partitioning is an open challenge in current ecological studies (Alder et al., 2013). Some of the highest priorities for the future research in this field are to disentangle the interaction between environmental heterogeneity and plant's trait variations and to allow the quantification of species responses to environmental changes in presence of competition and also in the absence of competition to reach a global understanding of niche partitioning (Alder et al. 2013). Defining niche as the environmental conditions where the average of absolute fitness of individuals of the species is optimum (Kearney, 2006), implies that the niche of one determined species would be the site where the environmental conditions let the optimal species function. At this regard, plant elemental composition, both in concentration and proportions of the main bioelements (C, N, P, K, Ca, Mg, S), represents the summary of a species' final optimum adaptation to its characteristic habitat with its specific abiotic and biotic conditions. Each nutrient has a different functional and morphological uses and each plant function uses nutrients in different proportions. Since each species has a different optimum morphology and functioning (metabolism and physiology), each species has a different use of the main different bioelements, e.g. faster growth rates should be associated with: larger N and mainly larger P concentrations and consequently with low N:P ratios (Sterner and Elser 2002); high capacity of water-use efficiency and water retention capacity with a high C:nutrients ratio; and high C and K concentrations and allocation capacity to photosynthetic tissues (Sardans and Peñuelas 2007; Babita et al. 2010; Laus et al. 2011; Oddo et al. 2011; Rivas-Ubach et al. 2012; Sardans et al. 2012b; Sardans and Peñuelas 2013). Thus, species' elemental composition should be determined, at least in part, by long-term genetic adaptation to a particular abiotic environment and also to its adaptation to its specific ecological strategy such as the optimal successional stage. However, some degree of flexibility is necessary for plant species' success by allowing the plant to respond to abiotic and biotic shifts.

We hypothesised that there are optimal elemental species' concentrations and elemental allocation patterns to different functions and organs that are the consequence of not only the optimum adaptation to maximise species fitness in determined abiotic and biotic circumstances – i.e. the consequence of long-term genetic adaptation – but also of short-term capacity to respond under certain limits to life-time environmental competition shifts. As a result, different plant species coexisting in the same biome, at least during some periods of their life, should have different elemental compositions thus contributing to diminishing the direct competition when growing together by competing for different elements with different intensity. Thus we propose the use of "biogeochemical niche" for each species as a holistic approach that not only take into account the soil traits in relation with nutrient availability but the final use of nutrients as consequence of the overall plant function in a determined global set of environmental conditions. Thus we understand "biogeochemical niche" as the region occupied in the multivariate space generated by the concentration and ratios of macronutrient and micronutrients in plant tissues (Peñuelas et al. 2008, 2010). This holistic view assumes that different plant species have a differential proportional use of elements in response to long-term evolutionary adaptation but also as a result of their flexibility to respond to current environmental changes.

How terrestrial plant species are able to modify their stoichiometry in response to environmental changes is a key unresolved question. Terrestrial plants have high stoichiometry flexibility compared with other ecological groups such as consumers (Sistla and Schimal 2012; Sardans et al. 2012a) due to the high capacity of nutrient allocation and retranslocation to different organs (Sistla and Schimal 2012). Indeed, the stoichiometrical flexibility of plant species can avoid direct competition.

We have used the Catalan Forest Inventory (CFI) to study the elemental concentrations (C, N, P, K, S, Mg and Ca) of leaves and wood as well as the mineralomasses (by considering the foliar and wood biomass) and the element allocation to different aboveground organs as a characterisation of the species biogeochemical niche. We have also used the CFI to study the relationships of the biogeochemical niche with climatic gradients in different biomes – the Mediterranean, the transition Mediterranean-wet temperate, the wet temperate and the subalpine – to study the relationships of the “biogeochemical niche” with different taxonomic groups (angiosperms and gymnosperms) and finally to compare the different biogeochemical niches of the different species of the same biome that frequently coexist at least during some successional stages. In this study we have aimed to study the role of (i) climatic biome and forest type, and (ii) taxonomy on the species biogeochemical niche segregation.

## Methods

Study area and climatic data

The study was based upon data in the Ecological Forest Inventory of Catalonia (Gracia et al. 2004) and the Third Spanish National Forest Inventory (Villaescusa and Díaz 1998; Villanueva 2005). These databases contain foliar C, N, P, K, S, Ca and Mg concentrations for the dominant tree species of 2854 plots, and of concentrations of the same element in branches, stems and leaves in a subset of 1004 plots together with the corresponding biomasses. In the most of the cases the species sampled was the dominant one. In some cases with two or three codominant species only one was aleatory sampled. These plots were uniformly distributed throughout the forested areas of Catalonia that cover 19568 $Km^2$. Catalonia, which has a surface area of 32114 $Km^2$, is located on the shores of the Mediterranean Sea, and the presence of the Pyrenees and continental gradients generate contrasting climatic regions, including semi-arid-Mediterranean, wet-Mediterranean, Atlantic wet temperate and Alpine. While coastal areas have Mediterranean climates, inland areas have mostly continental Mediterranean climates. To the north, the Pyrenees have montane or, at the highest elevations, alpine climates. All georeferenced data were processed using MiraMon 6.0 (Pons 2009). Data for mean annual precipitation (MAP) and mean annual temperature (MAT) were obtained from the "Atlas climàtic digital de Catalunya".

Estimation of biomass and growth

In each plot, all living trees with a diameter at breast height (DBH) of at least 5 cm were measured. Their species identity was annotated, and their height and DBH measured. Stem wood biomass (B) was estimated using the equation:

$$B = \pi(DBH/2)^2 \cdot H \cdot K \cdot D_w$$

where DBH is the tree diameter without bark at breast height, H is the tree height, K is the tapering, and Dw is the wood density. The K values were obtained from the measurements of the 4-8 most representative trees of the dominant species of each plot using the Bitterlich relascope. The current biomass (t ha$^{-1}$) per plot of the other aboveground organs of the different species was estimated using allometric equations obtained for each species and regionally (Vilà et al. 2003). Total wood per tree was the sum of branch and stem wood.

Sampling and chemical analyses

Leaves from each of the 2854 plots included in this study were collected. In each plot, we analysed samples of leaves, stems and branches for a plot. These samples were the result of combining the samples of the leaves, branches and stems, respectively, of at least three different trees collected and sampled in all directions of the canopy. The leaves were sampled in the upper middle part of the crown by using extensible loppers. The final foliar sample included all foliar cohorts present in the different branches sampled from the different trees selected. For more information on the method of sampling, see Vilà et al. (2003).

Samples were ground with a Braun Mikrodismembrator-U (B. *Braun* Biotech International, Melsungen, Germany). For the analyses of C and N, 1-2 mg of the pulverised, dried sample was combined with 2 mg of $V_2O_5$, which served as an oxidant. Concentrations of C and N were determined by combustion coupled to gas chromatography using a Thermo Electron Gas Chromatograph (model NA 2100, C.E. instruments-Thermo Electron, Milan, Italy). To determine the concentrations of P, samples were solubilised in 50 mL Teflon centrifuge tubes (Nalge Nunc International, Rochester, NY, USA) using an acid mixture of $HNO_3$ (60%) (143255, *purissimum*, PANREAC, Barcelona) and $HClO_4$ (60%) (141054, *purissimum*, PANREAC, Barcelona) (2:1) in a microwave oven (SAMSUNG, TDS, Seoul, South Korea). Two mL of the acidic solution were used per 100 mg of dry biomass of each sample. The digested samples were brought to a final volume of 10 mL by adding 3% $HClO_4$. Blank solutions (2 mL of the acid mixture with no sample biomass) were analysed in duplicate in each group of sample digestions. To assess the accuracy of the digestions and analytical procedures, we used a standard certified biomass (DC73351, poplar leaf, China National Analysis Centre for Iron & Steel). After digestion, the concentrations of P were determined using ICP-OES (Optic Emission Spectroscopy with Inductively Coupled Plasma) (JOBIN YBON JI 38 Jobin, France).

Variables and species studied

The dependent variables list used in ordination analyses are described in Table 1. We first analysed a set of foliar elemental concentration of C, N, P, K, S, Ca and Mg and the concentration ratio between the three main bioelements N:P, N:K and P:K in 2854 different forest plots representative of the main forest groups of Catalonia. These plots were dominated by the 15 tree species most abundant in the studied region; eight typical Mediterranean tree species and seven typical transition Mediterranean-wet temperate, and wet-temperate and alpine non-Mediterranean tree species.

We analysed a second set of variables (Table 1) in a set of 1004 forest plots. In these plots the available data on biomass of different aboveground organs (foliar and wood) allowed the calculation of elemental mineralomasses in different organs and the element ratios in foliar and wood biomass and also in total aboveground biomass (Table

1). We also calculated the foliar:wood content ratio of the seven elements studied. We conducted a PCA analysis with the C, N, P, K, S, Ca and Mg concentrations and the N:P, N:K and P:K concentration ratios of leaves, branches and stem, and the foliar:wood content ratio of the seven elements studied. This set of variables provides information not only of the stoichiometry of the main aboveground organs but also provides information of the different elemental allocation to the photosynthetic organ (leaves) relative to the structural-storing organ (wood).

Statistical analyses

Principal component analyses (PCA) and discriminant functional analysis (DFA) were performed to determine whether the concentrations and their stoichiometries and their allocation between leaves and wood could discriminate among climate and taxonomy (including differences at species level). Both ordination analysis are complementary (Johnson et al., 2003; Elliot et al., 2007; Qadir et al., 2008; Stamova et al., 2009). DFA is a supervised statistical algorithm that will derive an optimal separation between groups established a priori by maximizing between-group variance while minimizing within-group variances (Raamsdonk et al. 2001) whereas PCA does not maximize between-groups variation against within-group variance. Thus we have centred in the use of DFA is better to detect the variables that are more responsible of the differences among groups, while PCA allows to detect overall differences among groups and has been used to reinforce DFA. According with the “biogeochemical niche” hypothesis we tested the differences in elemental chemical composition of the main tree species of Catalan forests corresponding to different climates (defined by MAP and MAP), types classified here as Mediterranean (Mediterranean gymnosperms and Mediterranean evergreen angiosperms), transition Mediterranean-wet temperate and non-Mediterranean species (wet-temperate and alpine) and different taxonomical groups (angiosperms versus gymnosperms). In concrete we analyze this by performing four different DFA and corresponding PCA analyses. The first DFA and PCA were done with foliar data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K) that included 2854 plots dominated by the 19 most representative forest species of Catalonia allowing the comparison of global foliar elemental composition among different forest and taxonomy groups.

A second DFA were done with foliar data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K) of Mediterranean forest that included 1835 plots dominated by the seven most representative Mediterranean forest tree speices of Catalonia to test for differences in foliar composition and stoichiomtry among species that frequently coexist and competer among them.

The third DFA and the corresponding PCA analyses were done with foliar and branches and stem data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K and the foliar:wood content ratio of the seven elements) that included all species spread by 1004 plots that comprised data of biomass and foliar and wood chemical information dominated by the 15 most representative forest species of Catalonia allowing the comparison of global foliar elemental composition among different forest and taxonomy groups.

The fourth DFA were done with foliar and branches and stem data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K and the foliar:wood content ratio of the seven elements) of Mediterranean forest that included 667 plots dominated by the seven most representative Mediterranean forest tree speices of Catalonia to test for differences in foliar composition and stoichiomtry among species that frequently coexist and competer among them. In the third and fourth DFA, we used not only leaf chemical data but also the branches and stem concentrations and N:P, N:K and P:K ratios and the allocation of different elements between foliar and wood biomass. In the multiple correlations between PC scores and variables we used false discovery rate to correct the alpha-inflation (García 2004). The analyses were performed using Statistica 6.0 (StatSoft, Inc. Tule, Oklahoma, USA).

**Results**

Foliar stoichiometry

Typical Mediterranean species were significantly separated from non-Mediterranean species for MAT and mainly for MAP, with Mediterranean species living in plots with higher MAT and lower MAP than non-Mediterranean species (Figure S1, supplementatry material). The elemental concentrations, contents and ratios were different among the five different studied forest groups (Table S1, supplementatry material). Foliar nutrient concentrations were higher in wet temperate angiosperms and in transition Med-temp angiosperms than in the other forests groups (Table S1). Wet temperate angiosperms had the lowest allocation of nutrients to leaves with respect to wood despite their high foliar concentration; this was due to their lower foliar:wood content ratio (data not shown).

In the DFA done with foliar data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K) that included all species angiosperms were statistically separated from gymnosperms along Root 1 (that explains the 100% of the variance) ($F = 321$, $P < 0.0001$) (Figure 1). Moreover, the different forest groups were separated by the DFA (Figure 1, Table 2 and 3), with non-Mediterranean species having higher N, P and K, and lower C concentrations. This effect of climate was underlying the separation of Mediterranean and alpine species from wet temperate and transition Mediterranean-wet temperate angiosperms species and also of gymnosperm from angiosperm species (Figure 1, Tables 3 and 4). All the species were separated from each other by at least one of the four first PC axes (data not shown). All the studied species were separated by the DFA analysis (Figure 1, Tables 3 and 4). Foliar C, N, P, Ca and Mg concentrations were the variables with greatest discriminatory power of the model (Figure 1, Tables 3 and 4) in the separation among different forest groups. PCA analyses results are consistent with the results observed in the DFA. Within angiosperms the three different forest groups (Mediterranean evergreen angiosperms, wet temperate angiosperms and transition Mediterranean-wet temperate angiosperms) were separated along PC2 (Figure S2). MAP was significantly related to the scores of PC2 (R = 0.26, $P < 0.0001$) (Table S2). For the statistics of the regressions of the different variables with the first four PC axis scores see Table S4 (supplementary material). The first four PC axes were all them correlated significantly with leaf N, P and Ca concentrations and with foliar N:K and P:K concentration ratio (Table S2).

The standardized coefficients of the different variables in the Roots obtained with grouping angiosperms versus gymnosperms, different forest groups and different species are showed in Tables S3-S5, respectively. Elemental N, P, K, Mg, Ca contents in leaves and N. Mg, Ca and K foliar:wood content ratios were significantly related with the significant differences among forests groups and practically all studied variables were significantly related  with the observed significant separation among different studued species (Figure 2, Table 5).

When we focused on the Mediterranean species, which frequently coexist and are competing among them, we onserved that all pairwises were separated by the DFA (Figure 1, Tables 3 and 4). When we conducted the DFA analysis with only the Mediterranean species we also observed a separation among all the pairwise species (Table S6).

Global aboveground stoichiometry and element leaf:wood allocation

In the DFA analysis conducted with foliar and branches and stem data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K and the foliar:wood content ratio of the seven elements) differences between angiosperms versus gymnosperms, among different forests groups and studied species were observed in all cases and pairwise comparisons (Figure 2, Tables 5, 6 and S5). All the species were separated from each other by at least one of the three first PCs (data not shown), and most of them were separated with respect to each other by at least one of the first two PCs (Figure S3). Moreover, a strong significant difference between angiosperms and gymnosperms along PC1 was observed ($F = 1933$, $P < 0.0001$) (Figure S3), an effect related to high element allocation to leaves but also to higher C concentrations and N:P ratios in all aboveground organs in gymnosperns compared to angiosperms (Figure S3). For the statistics of the regressions of the different variables with the first four PC axis scores see Table S7 (supplementary material). The stem C concentrations, branch C, P, Ca and Mg concentrations, foliar Ca, K concentrations, N:P leaf, stem and branch content ratios, and C, P, Ca and K foliar:wood content ratio were significantly related with the significant differences between angiosperms and gymnosperms (Figure 2, Table 5). All the five studied forest groups were separated by the DFA analysis (Figure 2, Tables 5 and S4) and the model was significant (Wilk's =0.075, $F=23.7$, $P<0.0001$). Stem C, N, K and Ca contents, N (K and N:P stem contents ratios and Ca, K, P, Mg, S and C foliar:wood content ratios were the variables with greatest discriminatory power of the model (Lower partial Lambda, Figure 2, Tables 5 and S4) in the separation among different forest groups. The standardized coefficients of the different variables in the Roots obtained with grouping angiosperms versus gymnosperms, different forest groups and different species are showed in Tables S8-S10, respectively.

When we focused within Mediterranean species, which frequently coexist and are competing among them we observed that all pairwises were separated by the DFA (Figure 2, Tables 5 and 7). When we conducted the DFA analysis with only the Mediterranean species we also observed a separation among all the pairwise species (Table S11).

**Discussion**

The results demonstrated that the elemental composition partially depends on climate conditions. The forest tree species of drier-hotter areas (in this case Mediterranean species) and of colder sites (alpine) have on average higher C concentrations and C leaf:wood ratio and lower N, P and K leaf concentrations than wet temperate and transition Med-Temp tree species growing in less extreme climatic situations. The results agree with the fact that Mediterranean plants are, in general, drought tolerant with a high leaf C:N ratio (Sardans et al. 2008; Sardans et al. 2012c), have a high content of C-rich anti-stress compounds such as phenolics (Hernandez et al. 2004) and also have a high content of C-rich high-weight molecular groups, such as cellulose or lignin, which provide protection to water stress and loss (Pena-Rojas et al. 2005; Lee et al. 2012). Cold-stress adaptation has been related to higher content of C-rich metabolites such as fatty acids, sugars and derivates from the Krebs Cycle (Petrov et al. 2011; Sardans et al. 2011b and references within). Moreover, gymnosperms frequently have higher C concentrations and lower nutrient concentrations than angiosperm trees (Sardans et al. 2011a; Mediavilla et al. 2012) and the acicular form of their needles together with their rigid cuticle allow adaptation to drought and cold (Sakai 1983; Howe et al. 2003; Bréda et al. 2006). In general, higher leaf mass area related to high content of C-rich structural molecules is related to higher capacity to adapt to low temperatures (Ogaya and Peñuelas 2007). In spite of the great effect of taxonomy (gymnosperms versus angiosperms) in determining the tree elemental composition, the results also showed that within each group, and mainly within angiosperms, there was a clear relationship of tree stoichiometry with climate, especially with MAP.

There was higher allocation of all elements to leaves in gymnosperms than in angiosperms but with a higher proportion of C that consequently implies lower N, P and

K concentrations mainly in branches and stem than in angiosperms. The long-term evolutionary divergence of these two taxonomical groups, which frequently implied different functions and ecological roles, should underlie these general different elemental stoichiometry and allocation patterns between these two groups.

This study of seven typical dominant Mediterranean species shows that species of the same climatic-biome have different elemental compositions beyond the taxonomic group. Within each climate condition, the different species tend to dominate in different successional stages and/or in different microclimatic and edaphic conditions but also frequently coexist in the same community. Thus, the results provide solid evidence that the species' different optimal function and structure is linked to different use of bioelements supporting the idea of the biogeochemical niche as the place occupied in the multivariate space generated by the concentrations of macronutrient and micronutrients and their stoichiometric relationships and allocation to different plant tissues (Peñuelas et al. 2008, 2010). The results also suggest that this species-specific biogeochemical niche should be the final result of the species adaptation to abiotic factors such as climate and to biotic factors such as interspecific competition, the adaptation to different styles of life and successional stage, to different strategies to water and nutrient uptake, to different soil space and/or time exploitation and probably to different strategies for capture light. Thus, species should have a strong genetic elemental stoichiometry determination due to their long-term adaptation to abiotic and biotic specific environments that have end up generating an optimum metabolic and physiological function and an optimum morphological structure that in turn determine a specific use of nutrients. This fact should also allow the plants to partially avoid direct competition thus improving the possibilities of different species coexistence.

The capacity of a species to change its biogeochemical niche, and therefore the use of soil resources in different competitive states, is related to the capacity of species to adapt to survival in the ecosystem with higher diversity through an optimization in the efficiency of nutrient exploitation and therefore on the competitive ability .

Different plant species should also have a trade-off between their capacity of stoichiometry homeostasis to maintain their specific composition and some degree of flexibility. Species adapted to poor environments with lower capacity of nutrient uptake and higher nutrient use efficiency (for example, *Q. ilex*) have more homeostatic capacity (here represented by low variability in the PC space) linked to their lack of capacity to take up resources and to respond to nutrient pulses and to their high capacity to reduce nutrient losses (Aerts 1999). In contrast, species of nutrient-rich environments (for example, *F. sylvatica*) with higher capacities of taking up resources have higher stoichiometry flexibility (here represented by high variability in the PC space) linked to their higher capacity of adaptation to the changes in sources availability (Aerts 1999).

**Conclusions**

The results of this study of 2854 forest plots of the Catalonian Forest Inventory show that climate, taxonomy and competition combine to determine an optimum species biogeochemical niche corresponding to the optimal elemental concentrations and allocation to the different functions and structures of each species in each environment.

1.Forest tree species of hotter-drier environments have lower foliar N, P and K concentrations than species from cooler-wetter environments. On average trees of different forest groups have different foliar composition and different foliar:wood nutrient allocation.

2. Different taxonomical groups have different elemental composition mainly due to a proportionally higher elemental allocation to leaves than to wood, higher proportion of C than the other elements, and lower N, P and K concentrations mainly in stem and branches in gymnosperms than in angiosperms. Gymnosperms also have a higher nutrient foliar:wood content ratio than angiosperms.

3. Each forest type has different elemental composition and within each forest type, the different species have also different elemental composition suggesting a species-specific use of nutrients leading to the occupation of a different “biogeochemical niche”.

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Table 1. Sets of dependent variables and species studies in the ordination analyses.

| Sets of variables studies by ordination analysis | Mediterranean species | Transition Mediterranean-wet temperate | Temperate and alpine |
|---|---|---|---|
| **Foliar C, N, P, K, S, Ca and Mg concentrations and foliar N:P, N:K and P:K concentration ratios** | **Angiosperms**: *Arbutus unedo*, *Querucs ilex*, *Quercus suber*.<br><br>**Gymnosperms**: *Pinus halepensis*, *Pinus pinaster*, *Pinus pinea*, *Pinus nigra*. | **Angiosperms**: *Castanea sativa*, *Quercus canariensis*, *Quercus cerrioides*, *Quercus cerrioides x humilis*, *Quercus faginea*, *Quercus humilis* | **Angiosperms**: *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus petraea*.<br><br>**Gymnosperms**: *Abies alba*, *Pinus sylvestris*, *Pinus uncinata*. |
| **Foliar, wood and aboveground C:N, C:P, C:K, N:P, N:K and P:K concentrations and content ratios, and leaf:wood content ratio of C, N, P, K, S, Ca and Mg** | **Angiosperms**: *Arbutus unedo*, *Querucs ilex*, *Quercus suber*.<br><br>**Gymnosperms**: *Pinus halepensis*, *Pinus pinaster*, *Pinus pinea*, *Pinus nigra*. | **Angiosperms**: *Castanea sativa*, *Quercus canariensis*, *Quercus cerrioides*, *Quercus humilis* | **Angiosperms**: *Fagus sylvatica*, *Quercus petraea*.<br><br>**Gymnosperms**: *Pinus sylvestris*, *Pinus uncinata*. |

Table 2. Squared Mahalanobis distances among different forest groups in the discriminant functional analysis of foliar C, N, P, K, S, Ca and Mg concentrations and foliar N:P, N:K and P:K concentration ratios of the 2854 plots dominated by the 19 most representative forest species of Catalonia. All these distances were significantly greater than cero based on F test ($P < 0.001$).

| Ecotype groups | Med gymnosperms | Alpine gymnosperms | Transition Med-temp | Med. angiosperms evergreens |
|---|---|---|---|---|
| Wet temp. angiosperms | **38.2** | **32.3** | **2.99** | **16.5** |
| Med gymnosperms | | **2.65** | **25.1** | **6.43** |
| Alpine gymnosperms | | | **22.5** | **3.97** |
| Transition Med-temp | | | | **9.77** |

Table 3. Statistical results (Wilks' Lambda and P-value) of the discriminant functional analysis of foliar C, N, P, K, S, Ca and Mg concentrations and foliar N:P, N:K and P:K concentration ratios in the separation between angiosperms and gymnosperms, among forest groups and among studied species.

| Independent variables | Dependent variables of FDA analysis | | | | | |
|---|---|---|---|---|---|---|
| | **Separation between angiosperms and gymnosperms** | | **Separation among different forest types** | | **Separation among different species** | |
| | Wilks' Lambda | *P*-level | Wilks' Lambda | *P*-level | Wilks' Lambda | *P*-level |
| C | **0.514** | **<0.000001** | **0.227** | **<0.000001** | **0.090** | **<0.000001** |
| N | **0.494** | **<0.000001** | **0.227** | **<0.000001** | **0.092** | **<0.000001** |
| P | 0.470 | 0.37 | 0.200 | 0.27 | **0.083** | **<0.000001** |
| N:P | **0.476** | **<0.000001** | **0.207** | **<0.000001** | **0.085** | **<0.000001** |
| N:K | **0.470** | **0.026** | 0.201 | 0.055 | **0.079** | **<0.000001** |
| P:K | 0.470 | 0.11 | **0.203** | **<0.000001** | **0.081** | **<0.000001** |
| S | 0.470 | 0.25 | **0.213** | **<0.000001** | **0.086** | **<0.000001** |
| Ca | **0.527** | **<0.000001** | **0.241** | **<0.000001** | **0.109** | **<0.000001** |
| Mg | **0.482** | **<0.000001** | **0.256** | **<0.000001** | **0.122** | **<0.000001** |
| K | **0.475** | **<0.000001** | **0.212** | **<0.000001** | **0.084** | **<0.000001** |

Table 4. Squared Mahalanobis distances among different studied species in the discriminant functional analysis of foliar C, N, P, K, S, Ca and Mg concentrations and foliar N:P, N:K and P:K concentration ratios of the 2854 plots dominated by the 19 most representative forest species of Catalonia. All distances are significantly higher than cero based on F test ($P < 0.001$).

| Apecies | P. halepensis | Pi. nigra | P.pinaster | P. pinea | P. sylvestris | P. uncinata | Q. faginea | Q. ilex | Q. petraea | Q. suber | A. unedo | C. sativa | F. sylvatica | F. excelsior | Q.cerrioides | Q. humilis | Q. canariensis | Q. humilisxcerr |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A. alba | 15.8 | 15.3 | 23.9 | 32.7 | 11.1 | 15.3 | 24.7 | 10.2 | 39.8 | 16.4 | 8.71 | 54.1 | 38.7 | 99.5 | 25.5 | 18.9 | 34.2 | 35.6 |
| P.halepensis | | 5.12 | 3.52 | 5.89 | 5.87 | 10.4 | 25.7 | 7.16 | 39.3 | 11.4 | 9.101 | 36.9 | 44.4 | 89.8 | 24.5 | 25.6 | 30.5 | 38.36 |
| P. nigra | | | 5.00 | 9.34 | 1.62 | 1.35 | 36.0 | 8.42 | 47.9 | 11.3 | 10.91 | 49.0 | 51.7 | 112 | 36.4 | 33.8 | 38.1 | 50.36 |
| P. pinaster | | | | 2.13 | 7.41 | 10.0 | 29.5 | 10.0 | 44.4 | 13.2 | 13.7 | 38.2 | 51.6 | 93.6 | 24.9 | 32.1 | 34.6 | 45.7 |
| P. pinea | | | | | 11.2 | 15.8 | 29.3 | 12.6 | 42.3 | 14.6 | 16.7 | 32.4 | 49.1 | 86.5 | 27.7 | 33.0 | 31.8 | 44.5 |
| P. sylvestris | | | | | | 2.37 | 25.5 | 3.99 | 33.7 | 5.08 | 5.577 | 39.1 | 37.2 | 93.9 | 29.6 | 22.8 | 26.6 | 36.3 |
| P. uncinata | | | | | | | 41.2 | 10.6 | 51.9 | 12.6 | 14.0 | 56.5 | 54.9 | 120 | 43.1 | 37.2 | 42.0 | 55.3 |
| Q. faginea | | | | | | | | 13.3 | 6.84 | 11.4 | 12.8 | 14.6 | 10.7 | 34.0 | 6.72 | 4.13 | 6.19 | 6.30 |
| Q. ilex | | | | | | | | | 22.1 | 2.86 | 2.54 | 30.9 | 22. | 75.0 | 16.1 | 10.8 | 15.0 | 22.7 |
| Q. petraea | | | | | | | | | | 14.2 | 18.6 | 10.3 | 7.94 | 24.6 | 22.3 | 8.39 | 5.35 | 2.37 |
| Q. suber | | | | | | | | | | | 4.73 | 21.77 | 18.6 | 61.3 | 19.5 | 10.8 | 10.3 | 18.0 |
| A. unedo | | | | | | | | | | | | 25.7 | 20.0 | 70.7 | 17.4 | 8.74 | 14.6 | 17.8 |
| C. sativa | | | | | | | | | | | | | 19.7 | 28.5 | 27.5 | 19.1 | 9.87 | 14.0 |
| F. sylvatica | | | | | | | | | | | | | | 49.8 | 25.3 | 7.54 | 3.08 | 11.3 |
| F. excelsior | | | | | | | | | | | | | | | 53.1 | 46.6 | 41.8 | 21.9 |
| Q. cerrioides | | | | | | | | | | | | | | | | 9.63 | 18.3 | 19.9 |
| Q. humilis | | | | | | | | | | | | | | | | | 5.97 | 7.45 |
| Q. canariensis | | | | | | | | | | | | | | | | | | 9.53 |

Table 5. Statistical results (Wilks' Lambda and P-value) of the discriminant function of C, N, P, K, S, Ca and Mg concentrations and N:P, N:K and P:K concentration ratios of leaves, branches and stems, and the foliar:wood content ratio of the seven elements studied in the separation between angiosperms and gymnosperms, among forest groups and among studied species.

| Independent variables | Dependent variables of FDA analysis | | | | | |
|---|---|---|---|---|---|---|
| | **Separation between angiosperms and gymnosperms** | | **Separation among different forest types** | | **Separation among different species** | |
| | Wilks' Lambda | *P*-level | Wilks' Lambda | *P*-level | Wilks' Lambda | *P*-level |
| C concentration stems | **0.282** | **<0.000001** | **0.0857** | **<0.000001** | **0.00378** | **<0.000001** |
| N concentration stems | **0.282** | **<0.000001** | **0.0799** | **<0.000001** | **0.00359** | **<0.000001** |
| P concentration stems | 0.275 | 0.059 | **0.0778** | **0.048** | **0.00337** | **0.000078** |
| S concentration stems | 0.275 | 0.26 | 0.0776 | 0.16 | 0.00329 | 0.079 |
| Ca concentration stems | 0.275 | 0.10 | **0.0801** | **<0.000001** | **0.00339** | **0.000007** |
| Mg concentration stems | 0.275 | 0.12 | **0.0780** | **0.020** | **0.00334** | **0.00097** |
| K concentration stems | **0.280** | **0.000005** | **0.0798** | **0.000001** | **0.00348** | **<0.000001** |
| C concentration branches | **0.288** | **<0.000001** | **0.0888** | **<0.000001** | **0.00457** | **<0.000001** |
| N concentration branches | 0.275 | 0.12 | 0.0774 | 0.30 | 0.00330 | 0.054 |
| P concentration branches | **0.279** | **0.000030** | **0.0789** | **0.00013** | **0.00343** | **<0.000001** |
| S concentration branches | 0.274 | 0.73 | 0.0772 | 0.73 | 0.00327 | 0.39 |
| Ca concentration branches | 0.274 | 0.43 | **0.0781** | **0.011** | **0.00335** | **0.00034** |
| Mg concentration branches | 0.274 | 0.61 | **0.0808** | **<0.000001** | **0.00354** | **<0.000001** |
| K concentration branches | **0.280** | **0.000004** | **0.0812** | **<0.000001** | **0.00351** | **<0.000001** |
| C concentration leaves | **0.293** | **<0.000001** | **0.0922** | **<0.000001** | **0.00529** | **<0.000001** |
| N concentration leaves | **0.280** | **0.000014** | **0.0805** | **<0.000001** | **0.00361** | **<0.000001** |
| P concentration leaves | **0.281** | **0.000001** | **0.0802** | **<0.000001** | **0.00342** | **<0.000001** |
| S concentration leaves | 0.275 | 0.051 | **0.0785** | **0.0013** | **0.00345** | **<0.000001** |
| Ca concentration leaves | **0.281** | **0.000002** | **0.0797** | **0.000001** | **0.00364** | **<0.000001** |
| Mg concentration leaves | 0.274 | 0.51 | **0.0789** | **0.00014** | **0.00365** | **<0.000001** |
| N:P leaf concentration | **0.282** | **<0.000001** | **0.0817** | **<0.000001** | **0.00344** | **<0.000001** |
| N:K leaf concentration | **0.279** | **0.000024** | **0.0786** | **0.00069** | **0.00407** | **<0.000001** |
| P:K leaf concentration | 0.274 | 0.47 | 0.0776 | 0.14 | **0.00345** | **<0.000001** |
| N:P stems | 0.274 | 0.37 | 0.0777 | 0.068 | **0.00335** | **0.00032** |
| N:K stems | **0.280** | **0.000015** | **0.0790** | **0.000091** | **0.00338** | **0.000023** |
| P:K stems | **0.276** | **0.013** | **0.0781** | **0.0095** | **0.00347** | **<0.000001** |
| N:P branches | 0.274 | 0.36 | **0.0782** | **0.0045** | **0.00340** | **0.000002** |
| N:K branches | 0.275 | 0.093 | 0.0777 | 0.072 | **0.00332** | **0.011** |
| P:K branches | **0.282** | **<0.000001** | **0.0800** | **<0.000001** | **0.00332** | **0.013** |
| C (L/W) content ratio | **0.275** | **0.039** | **0.0861** | **<0.000001** | **0.00347** | **<0.000001** |
| N(L/W) content ratio | 0.275 | 0.071 | 0.0775 | 0.26 | **0.00374** | **<0.000001** |
| P(L/W) content ratio | **0.277** | **0.0017** | **0.0778** | **0.039** | **0.00335** | **0.00063** |
| S(L/W) content ratio | 0.275 | 0.24 | 0.0776 | 0.15 | **0.00341** | **0.000001** |
| Ca(L/W) content ratio | **0.277** | **0.00079** | **0.0851** | **<0.000001** | **0.00349** | **<0.000001** |
| Mg(L/W) content ratio | 0.274 | 0.41 | **0.0802** | **<0.000001** | **0.00378** | **<0.000001** |
| K(L/W) content ratio | **0.275** | **0.039** | **0.0783** | **0.0029** | **0.00395** | **<0.000001** |

Table 6. Test statistics for squared Mahalanobis distances among different forest groups in the discriminant functional analysis with C, N, P, K, S, Ca and Mg concentrations and N:P, N:K and P:K concentration ratios of leaves, branches and stems, and the foliar:wood content ratio of the seven elements studied as variables and the 1004 plots dominated by the 15 most representative forest tree species of Catalonia. All distances are significantly higher than cero based on F test (*P* < 0.001).

| Ecotype groups | Transition Med-temp | Wet temp. angiosperms | Med gymnosperms | Alpine gymnosperms |
|---|---|---|---|---|
| Med. Angiosperms evergreens | **9.90** | **24.1** | **12.5** | **15.5** |
| Transition Med-temp | | **22.5** | **14.2** | **15.9** |
| Wet temp. angiosperms | | | **31.3** | **27.5** |
| Med gymnosperms | | | | **3.47** |

Table 7. Test statistics for squared Mahalanobis distances among different studied species in the discriminant functional analysis with C, N, P, K, S, Ca and Mg concentrations and N:P, N:K and P:K concentration ratios of leaves, branches and stems, and the foliar:wood content ratio of the seven elements studied as variables and the 1004 plots dominated by the 15 most representative forest tree species of Catalonia. All distances are significantly higher than cero based on F test ($P < 0.001$).

| | *Pinus sylvestris* | *Pinus nigra* | *Pinus uncinata* | *Pinus pinaster* | *Quercus ilex* | *Pinus pinea* | *Castanea sativa* | *Arbutus unedo* | *Quercus canariensis x humilis* | *Quercus suber* | *Quercus cerrioides* | *Quercus humilis* | *Quercus petraea* | *Fagus sylvatica* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pinus halepensis* | 10.6 | 13.6 | 43.2 | 28.6 | 13.9 | 11.6 | 40.9 | 18.5 | 17.23831 | 32.48 | 78.1 | 17.6 | 37.8 | 37.5 |
| *Pinus sylvestris* | | 4.05 | 21.0 | 24.6 | 18.4 | 14.9 | 36.1 | 15.5 | 18.8 | 35.0 | 88.2 | 22.2 | 34.0 | 32.0 |
| *Pinus nigra* | | | 13.8 | 19.6 | 21.7 | 19.7 | 42.0 | 22.4 | 21.2 | 36.20 | 89.2 | 26.5 | 44.5 | 42.1 |
| *Pinus uncinata* | | | | 29.8 | 50.3 | 55.5 | 68.2 | 51.8 | 47.2 | 61.5 | 115 | 54.2 | 78.7 | 72.9 |
| *Pinus pinaster* | | | | | 26.3 | 37.0 | 40.1 | 39.8 | 32.4 | 43.7 | 88.4 | 36.8 | 64.5 | 58.7 |
| *Quercus ilex* | | | | | | 23.9 | 39.8 | 13.23 | 9.89 | 18.6 | 60.4 | 13.8 | 32.4 | 30.1 |
| *Pinus pinea* | | | | | | | 49.8 | 20.1 | 27.7 | 42.9 | 86.6 | 29.2 | 45.0 | 42.6 |
| *Castanea sativa* | | | | | | | | 39.2 | 26.5 | 54.7 | 108 | 42.2 | 46.9 | 48.6 |
| *Arbutus unedo* | | | | | | | | | 14.1 | 32.7 | 80.4 | 19.3 | 33.5 | 36.4 |
| *Quercus canariensis x humilis* | | | | | | | | | | 20.0 | 60.3 | 11.5 | 28.0 | 31.9 |
| *Quercus suber* | | | | | | | | | | | 68.0 | 23.0 | 38.5 | 35.49 |
| *Quercus cerrioides* | | | | | | | | | | | | 50.5 | 95.5 | 86.09 |
| *Quercus humilis* | | | | | | | | | | | | | 24.0 | 30.6 |
| *Quercus petraea* | | | | | | | | | | | | | | 16.0 |

## Figure captions

Figure 1. Biplots of roots of the results of the discriminant function of C, N, P, K, S, Ca and Mg concentrations and foliar N:P, N:K and P:K concentration ratios in the separation between angiosperms and gymnosperms (A), among forest groups (B) and among studied species (C).

Figure 2. Biplots of roots of the results of the discriminant function of C, N, P, K, S, Ca and Mg concentrations and N:P, N:K and P:K concentration ratios of leaves, branches and stems, and the foliar:wood content ratio of the seven elements studied in the separation between angiosperms and gymnosperms (A), among forest groups (B) and among studied species (C).

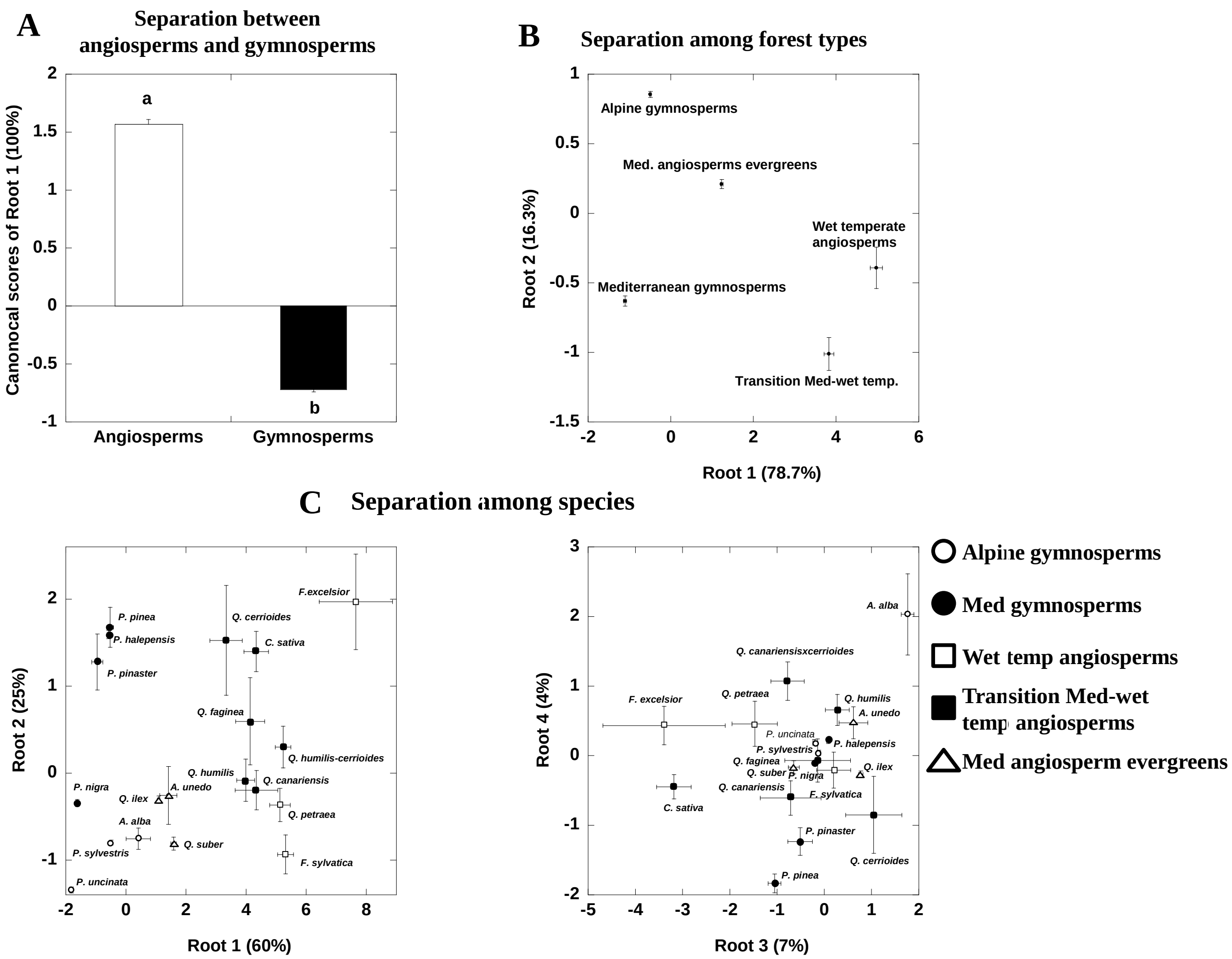
A
Separation between angiosperms and gymnosperms
Canonocal scores of Root 1 (100%)
a
b
Angiosperms
Gymnosperms
B
Separation among forest types
Root 2 (16.3%)
Root 1 (78.7%)
Alpine gymnosperms
Med. angiosperms evergreens
Wet temperate angiosperms
Mediterranean gymnosperms
Transition Med-wet temp.
C
Separation among species
Root 2 (25%)
Root 1 (60%)
Root 4 (4%)
Root 3 (7%)
P. pinea
P. halepensis
P. pinaster
Q. cerrioides
C. sativa
F.excelsior
Q. faginea
Q. humilis-cerrioides
Q. humilis
Q. canariensis
Q. petraea
P. nigra
Q. ilex
A. unedo
A. alba
P. sylvestris
Q. suber
F. sylvatica
P. uncinata
Q. canariensisxcerrioides
F. excelsior
Alpine gymnosperms
Med gymnosperms
Wet temp angiosperms
Transition Med-wet temp angiosperms
Med angiosperm evergreens

Figure 1

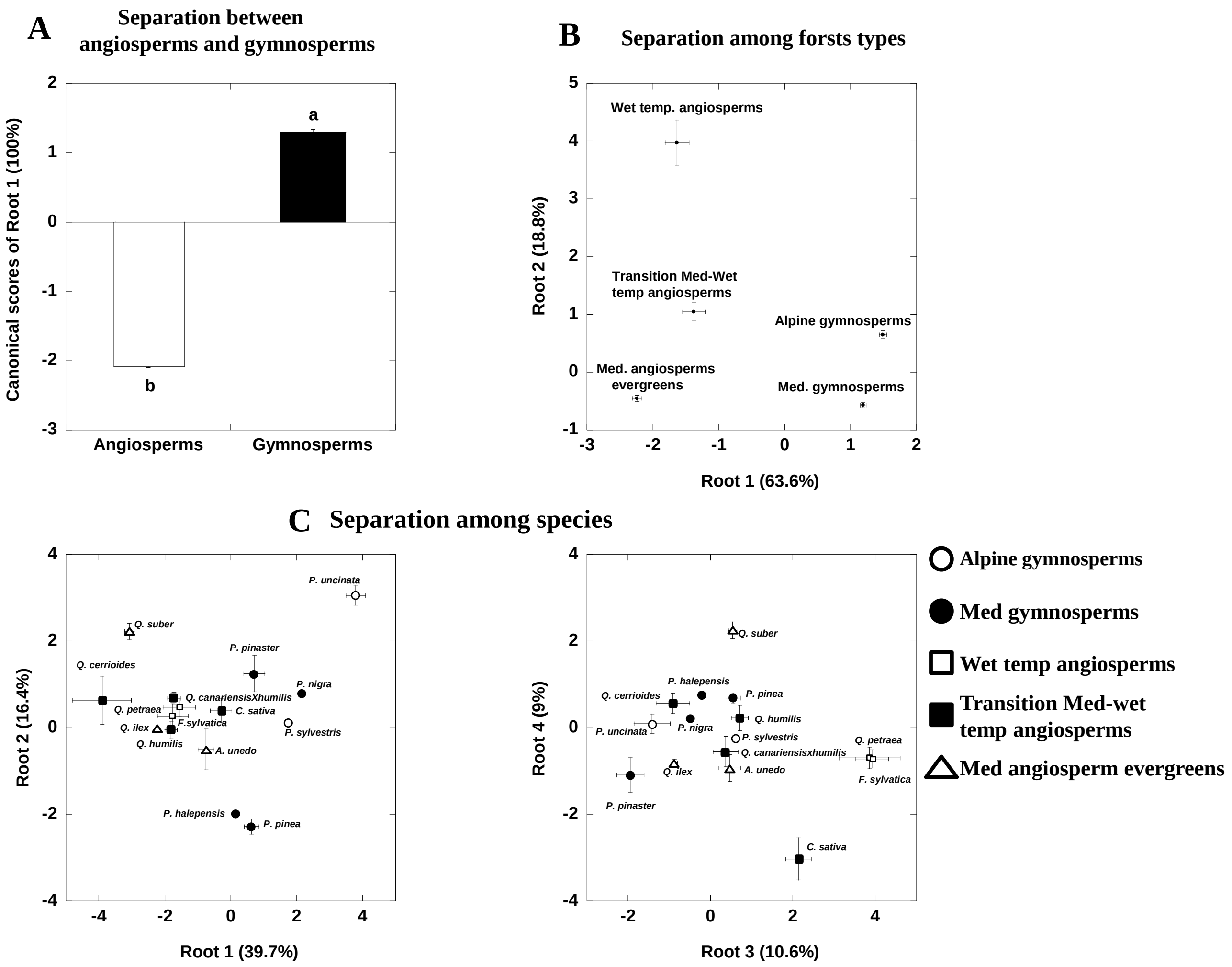
A
Separation between angiosperms and gymnosperms
Canonical scores of Root 1 (100%)
a
b
Angiosperms
Gymnosperms
B
Separation among forsts types
Root 2 (18.8%)
Root 1 (63.6%)
Wet temp. angiosperms
Transition Med-Wet temp angiosperms
Alpine gymnosperms
Med. angiosperms evergreens
Med. gymnosperms
C
Separation among species
Root 2 (16.4%)
Root 1 (39.7%)
Root 4 (9%)
Root 3 (10.6%)
P. uncinata
Q. suber
P. pinaster
Q. cerrioides
P. nigra
Q. canariensisXhumilis
Q. petraea
C. sativa
F.sylvatica
Q. ilex
P. sylvestris
Q. humilis
A. unedo
P. halepensis
P. pinea
F. sylvatica
Alpine gymnosperms
Med gymnosperms
Wet temp angiosperms
Transition Med-wet temp angiosperms
Med angiosperm evergreens

Figure 2