

1 **Climate and taxonomy underlie different elemental concentrations and**  
2 **stoichiometries of forest species: the optimum “biogeochemical niche”.**

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9

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

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

31

32 **Introduction**

33 Several studies have found strong relationships of climate and soil type gradients with  
34 the N:P ratio of terrestrial plants (Reich and Oleksyn 2004; Kerkhoff et al. 2005; Zheng  
35 and Shangguan 2007; Yuan and Chen 2009; Vitousek et al. 2010; Sardans et al. 2011a;  
36 Sardans and Peñuelas 2013) suggesting that terrestrial plant species should have an  
37 optimum N:P ratio enabling them to better adapt to their optimum abiotic niche  
38 (Sardans et al. 2012a). Moreover, apart from N and P, other elements such as K can be  
39 also limiting in terrestrial plant communities. Evidence of K limitation has been  
40 observed from temperate (Tripler et al. 2006) to tropical ecosystems (Tripler et al. 2006;  
41 Wright et al. 2011; Baribaut et al. 2012; Santiago et al. 2012). Although less than N, P  
42 and K, other nutrients such as S, Mg or Ca also become limiting in terrestrial plant  
43 communities (Hailes et al. 1997; Naples and Fisk 2010; Baribault et al. 2012; Lapeins et  
44 al. 2013). Thus a better understanding of variations in all essential plant nutrients and  
45 their critical relationships (rather than in N and P centric perspective) is essential in  
46 holistic biogeochemical models. Han et al. (2011) by analyzing 11 different nutrients in  
47 1900 plant species across China observed that all these elements were different in  
48 relation to climate, soil and functional type, showing the need of the use of most  
49 nutrients as possible to reach a more holistic approach to ecological plant nutrition  
50 knowledge and for the development of multiple elements biogeochemical models.

51         The study of the causes and factors that can help to understand niche partitioning  
52 is an open challenge in current ecological studies (Alder et al., 2013). Some of the  
53 highest priorities for the future research in this field are to disentangle the interaction  
54 between environmental heterogeneity and plant's trait variations and to allow the  
55 quantification of species responses to environmental changes in presence of competition  
56 and also in the absence of competition to reach a global understanding of niche

57 partitioning (Alder et al. 2013). Defining niche as the environmental conditions where  
58 the average of absolute fitness of individuals of the species is optimum (Kearney, 2006),  
59 implies that the niche of one determined species would be the site where the  
60 environmental conditions let the optimal species function. At this regard, plant  
61 elemental composition, both in concentration and proportions of the main bioelements  
62 (C, N, P, K, Ca, Mg, S), represents the summary of a species' final optimum adaptation  
63 to its characteristic habitat with its specific abiotic and biotic conditions. Each nutrient  
64 has a different functional and morphological uses and each plant function uses nutrients  
65 in different proportions. Since each species has a different optimum morphology and  
66 functioning (metabolism and physiology), each species has a different use of the main  
67 different bioelements, e.g. faster growth rates should be associated with: larger N and  
68 mainly larger P concentrations and consequently with low N:P ratios (Sterner and Elser  
69 2002); high capacity of water-use efficiency and water retention capacity with a high  
70 C:nutrients ratio; and high C and K concentrations and allocation capacity to  
71 photosynthetic tissues (Sardans and Peñuelas 2007; Babita et al. 2010; Laus et al. 2011;  
72 Oddo et al. 2011; Rivas-Ubach et al. 2012; Sardans et al. 2012b; Sardans and Peñuelas  
73 2013). Thus, species' elemental composition should be determined, at least in part, by  
74 long-term genetic adaptation to a particular abiotic environment and also to its  
75 adaptation to its specific ecological strategy such as the optimal successional stage.  
76 However, some degree of flexibility is necessary for plant species' success by allowing  
77 the plant to respond to abiotic and biotic shifts.

78         We hypothesised that there are optimal elemental species' concentrations and  
79 elemental allocation patterns to different functions and organs that are the consequence  
80 of not only the optimum adaptation to maximise species fitness in determined abiotic  
81 and biotic circumstances – i.e. the consequence of long-term genetic adaptation – but

82 also of short-term capacity to respond under certain limits to life-time environmental  
83 competition shifts. As a result, different plant species coexisting in the same biome, at  
84 least during some periods of their life, should have different elemental compositions  
85 thus contributing to diminishing the direct competition when growing together by  
86 competing for different elements with different intensity. Thus we propose the use of  
87 “biogeochemical niche” for each species as a holistic approach that not only take into  
88 account the soil traits in relation with nutrient availability but the final use of nutrients  
89 as consequence of the overall plant function in a determined global set of environmental  
90 conditions. Thus we understand “biogeochemical niche” as the region occupied in the  
91 multivariate space generated by the concentration and ratios of macronutrient and  
92 micronutrients in plant tissues (Peñuelas et al. 2008, 2010). This holistic view assumes  
93 that different plant species have a differential proportional use of elements in response  
94 to long-term evolutionary adaptation but also as a result of their flexibility to respond to  
95 current environmental changes.

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

102         We have used the Catalan Forest Inventory (CFI) to study the elemental  
103 concentrations (C, N, P, K, S, Mg and Ca) of leaves and wood as well as the  
104 mineralomasses (by considering the foliar and wood biomass) and the element  
105 allocation to different aboveground organs as a characterisation of the species  
106 biogeochemical niche. We have also used the CFI to study the relationships of the

107 biogeochemical niche with climatic gradients in different biomes – the Mediterranean,  
108 the transition Mediterranean-wet temperate, the wet temperate and the subalpine – to  
109 study the relationships of the “biogeochemical niche” with different taxonomic groups  
110 (angiosperms and gymnosperms) and finally to compare the different biogeochemical  
111 niches of the different species of the same biome that frequently coexist at least during  
112 some successional stages. In this study we have aimed to study the role of (i) climatic  
113 biome and forest type, and (ii) taxonomy on the species biogeochemical niche  
114 segregation.  
115

116 **Methods**

117 Study area and climatic data

118 The study was based upon data in the Ecological Forest Inventory of Catalonia (Gracia  
119 et al. 2004) and the Third Spanish National Forest Inventory (Villaescusa and Díaz  
120 1998; Villanueva 2005). These databases contain foliar C, N, P, K, S, Ca and Mg  
121 concentrations for the dominant tree species of 2854 plots, and of concentrations of the  
122 same element in branches, stems and leaves in a subset of 1004 plots together with the  
123 corresponding biomasses. In the most of the cases the species sampled was the  
124 dominant one. In some cases with two or three codominant species only one was  
125 aleatory sampled. These plots were uniformly distributed throughout the forested areas  
126 of Catalonia that cover 19568 Km<sup>2</sup>. Catalonia, which has a surface area of 32114 Km<sup>2</sup>,  
127 is located on the shores of the Mediterranean Sea, and the presence of the Pyrenees and  
128 continental gradients generate contrasting climatic regions, including semi-arid-  
129 Mediterranean, wet-Mediterranean, Atlantic wet temperate and Alpine. While coastal  
130 areas have Mediterranean climates, inland areas have mostly continental Mediterranean  
131 climates. To the north, the Pyrenees have montane or, at the highest elevations, alpine  
132 climates. All georeferenced data were processed using MiraMon 6.0 (Pons 2009). Data  
133 for mean annual precipitation (MAP) and mean annual temperature (MAT) were  
134 obtained from the “Atlas climàtic digital de Catalunya”.

135

136 Estimation of biomass and growth

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

140

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

142

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

#### 150 Sampling and chemical analyses

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

159 Samples were ground with a Braun Mikrodismembrator-U (B. *Braun* Biotech  
160 International, Melsungen, Germany). For the analyses of C and N, 1-2 mg of the  
161 pulverised, dried sample was combined with 2 mg of  $V_2O_5$ , which served as an oxidant.  
162 Concentrations of C and N were determined by combustion coupled to gas  
163 chromatography using a Thermo Electron Gas Chromatograph (model NA 2100, C.E.  
164 instruments-Thermo Electron, Milan, Italy). To determine the concentrations of P,  
165 samples were solubilised in 50 mL Teflon centrifuge tubes (Nalge Nunc International,



166 Rochester, NY, USA) using an acid mixture of HNO<sub>3</sub> (60%) (143255, *purissimum*,  
167 PANREAC, Barcelona) and HClO<sub>4</sub> (60%) (141054, *purissimum*, PANREAC,  
168 Barcelona) (2:1) in a microwave oven (SAMSUNG, TDS, Seoul, South Korea). Two  
169 mL of the acidic solution were used per 100 mg of dry biomass of each sample. The  
170 digested samples were brought to a final volume of 10 mL by adding 3% HClO<sub>4</sub>. Blank  
171 solutions (2 mL of the acid mixture with no sample biomass) were analysed in duplicate  
172 in each group of sample digestions. To assess the accuracy of the digestions and  
173 analytical procedures, we used a standard certified biomass (DC73351, poplar leaf,  
174 China National Analysis Centre for Iron & Steel). After digestion, the concentrations of  
175 P were determined using ICP-OES (Optic Emission Spectroscopy with Inductively  
176 Coupled Plasma) (JOBIN YBON JI 38 Jobin, France).

177

178 Variables and species studied

179

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

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

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

198

199 Statistical analyses

200

201 Principal component analyses (PCA) and discriminant functional analysis (DFA) were  
202 performed to determine whether the concentrations and their stoichiometries and their  
203 allocation between leaves and wood could discriminate among climate and taxonomy  
204 (including differences at species level). Both ordination analysis are complementary  
205 (Johnson et al., 2003; Elliot et al., 2007; Qadir et al., 2008; Stamova et al., 2009). DFA  
206 is a supervised statistical algorithm that will derive an optimal separation between  
207 groups established a priori by maximizing between-group variance while minimizing  
208 within-group variances (Raamsdonk et al. 2001) whereas PCA does not maximize  
209 between-groups variation against within-group variance. Thus we have centred in the  
210 use of DFA is better to detect the variables that are more responsible of the differences  
211 among groups, while PCA allows to detect overall differences among groups and has  
212 been used to reinforce DFA. According with the “biogeochemical niche” hypothesis we  
213 tested the differences in elemental chemical composition of the main tree species of  
214 Catalan forests corresponding to different climates (defined by MAP and MAP), types  
215 classified here as Mediterranean (Mediterranean gymnosperms and Mediterranean

216 evergreen angiosperms), transition Mediterranean-wet temperate and non-  
217 Mediterranean species (wet-temperate and alpine) and different taxonomical groups  
218 (angiosperms versus gymnosperms). In concrete we analyze this by performing four  
219 different DFA and corresponding PCA analyses. The first DFA and PCA were done  
220 with foliar data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K) that included 2854 plots  
221 dominated by the 19 most representative forest species of Catalonia allowing the  
222 comparison of global foliar elemental composition among different forest and taxonomy  
223 groups.

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

229 The third DFA and the corresponding PCA analyses were done with foliar and  
230 branches and stem data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K and the foliar:wood  
231 content ratio of the seven elements) that included all species spread by 1004 plots that  
232 comprised data of biomass and foliar and wood chemical information dominated by the  
233 15 most representative forest species of Catalonia allowing the comparison of global  
234 foliar elemental composition among different forest and taxonomy groups.

235 The fourth DFA were done with foliar and branches and stem data (C, N, P, K, S,  
236 Ca, Mg, N:P, N:K and P:K and the foliar:wood content ratio of the seven elements) of  
237 Mediterranean forest that included 667 plots dominated by the seven most  
238 representative Mediterranean forest tree speices of Catalonia to test for differences in  
239 foliar composition and stoichiometry among species that frequently coexist and compete  
240 among them. In the third and fourth DFA, we used not only leaf chemical data but also

241 the branches and stem concentrations and N:P, N:K and P:K ratios and the allocation of  
242 different elements between foliar and wood biomass. In the multiple correlations  
243 between PC scores and variables we used false discovery rate to correct the alpha-  
244 inflation (García 2004). The analyses were performed using Statistica 6.0 (StatSoft, Inc.  
245 Tule, Oklahoma, USA).  
246

247 **Results**

248

249 Foliar stoichiometry

250

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

261 In the DFA done with foliar data (C, N, P, K, S, Ca, Mg, N:P, N:K and P:K)  
262 that included all species angiosperms were statistically separated from gymnosperms  
263 along Root 1 (that explains the 100% of the variance) ( $F = 321$ ,  $P < 0.0001$ ) (Figure 1).  
264 Moreover, the different forest groups were separated by the DFA (Figure 1, Table 2 and  
265 3), with non-Mediterranean species having higher N, P and K, and lower C  
266 concentrations. This effect of climate was underlying the separation of Mediterranean  
267 and alpine species from wet temperate and transition Mediterranean-wet temperate  
268 angiosperms species and also of gymnosperm from angiosperm species (Figure 1,  
269 Tables 3 and 4). All the species were separated from each other by at least one of the  
270 four first PC axes (data not shown). All the studied species were separated by the DFA  
271 analysis (Figure 1, Tables 3 and 4). Foliar C, N, P, Ca and Mg concentrations were the  
272 variables with greatest discriminatory power of the model (Figure 1, Tables 3 and 4) in

273 the separation among different forest groups. PCA analyses results are consistent with  
274 the results observed in the DFA. Within angiosperms the three different forest groups  
275 (Mediterranean evergreen angiosperms, wet temperate angiosperms and transition  
276 Mediterranean-wet temperate angiosperms) were separated along PC2 (Figure S2).  
277 MAP was significantly related to the scores of PC2 ( $R = 0.26$ ,  $P < 0.0001$ ) (Table S2).  
278 For the statistics of the regressions of the different variables with the first four PC axis  
279 scores see Table S4 (supplementary material). The first four PC axes were all them  
280 correlated significantly with leaf N, P and Ca concentrations and with foliar N:K and  
281 P:K concentration ratio (Table S2).

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

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

294

295 Global aboveground stoichiometry and element leaf:wood allocation

296

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

321           When we focused within Mediterranean species, which frequently coexist and  
322 are competing among them we observed that all pairwise were separated by the DFA  
323 (Figure 2, Tables 5 and 7). When we conducted the DFA analysis with only the  
324 Mediterranean species we also observed a separation among all the pairwise species  
325 (Table S11).  
326



327 **Discussion**

328 The results demonstrated that the elemental composition partially depends on climate  
329 conditions. The forest tree species of drier-hotter areas (in this case Mediterranean  
330 species) and of colder sites (alpine) have on average higher C concentrations and C  
331 leaf:wood ratio and lower N, P and K leaf concentrations than wet temperate and  
332 transition Med-Temp tree species growing in less extreme climatic situations. The  
333 results agree with the fact that Mediterranean plants are, in general, drought tolerant  
334 with a high leaf C:N ratio (Sardans et al. 2008; Sardans et al. 2012c), have a high  
335 content of C-rich anti-stress compounds such as phenolics (Hernandez et al. 2004) and  
336 also have a high content of C-rich high-weight molecular groups, such as cellulose or  
337 lignin, which provide protection to water stress and loss (Pena-Rojas et al. 2005; Lee et  
338 al. 2012). Cold-stress adaptation has been related to higher content of C-rich  
339 metabolites such as fatty acids, sugars and derivatives from the Krebs Cycle (Petrov et al.  
340 2011; Sardans et al. 2011b and references within). Moreover, gymnosperms frequently  
341 have higher C concentrations and lower nutrient concentrations than angiosperm trees  
342 (Sardans et al. 2011a; Mediavilla et al. 2012) and the acicular form of their needles  
343 together with their rigid cuticle allow adaptation to drought and cold (Sakai 1983; Howe  
344 et al. 2003; Bréda et al. 2006). In general, higher leaf mass area related to high content  
345 of C-rich structural molecules is related to higher capacity to adapt to low temperatures  
346 (Ogaya and Peñuelas 2007). In spite of the great effect of taxonomy (gymnosperms  
347 versus angiosperms) in determining the tree elemental composition, the results also  
348 showed that within each group, and mainly within angiosperms, there was a clear  
349 relationship of tree stoichiometry with climate, especially with MAP.

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

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

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

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

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

390

## 391 **Conclusions**

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

396

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

401

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

407

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

411

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

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

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

Ecotype groups	Med gymnosperms	Alpine gymnosperms	Transition Med- temp	Med. angiosperms evergreens
Wet temp. angiosperms	<b>38.2</b>	<b>32.3</b>	<b>2.99</b>	<b>16.5</b>
Med gymnosperms		<b>2.65</b>	<b>25.1</b>	<b>6.43</b>
Alpine gymnosperms			<b>22.5</b>	<b>3.97</b>
Transition Med- temp				<b>9.77</b>

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595 Table 3. Statistical results (Wilks' Lambda and P-value) of the discriminant functional  
 596 analysis of foliar C, N, P, K, S, Ca and Mg concentrations and foliar N:P, N:K and P:K  
 597 concentration ratios in the separation between angiosperms and gymnosperms, among  
 598 forest groups and among studied species.  
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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	<b>0.514</b>	<b>&lt;0.000001</b>	<b>0.227</b>	<b>&lt;0.000001</b>	<b>0.090</b>	<b>&lt;0.000001</b>
N	<b>0.494</b>	<b>&lt;0.000001</b>	<b>0.227</b>	<b>&lt;0.000001</b>	<b>0.092</b>	<b>&lt;0.000001</b>
P	0.470	0.37	0.200	0.27	<b>0.083</b>	<b>&lt;0.000001</b>
N:P	<b>0.476</b>	<b>&lt;0.000001</b>	<b>0.207</b>	<b>&lt;0.000001</b>	<b>0.085</b>	<b>&lt;0.000001</b>
N:K	<b>0.470</b>	<b>0.026</b>	0.201	0.055	<b>0.079</b>	<b>&lt;0.000001</b>
P:K	0.470	0.11	<b>0.203</b>	<b>&lt;0.000001</b>	<b>0.081</b>	<b>&lt;0.000001</b>
S	0.470	0.25	<b>0.213</b>	<b>&lt;0.000001</b>	<b>0.086</b>	<b>&lt;0.000001</b>
Ca	<b>0.527</b>	<b>&lt;0.000001</b>	<b>0.241</b>	<b>&lt;0.000001</b>	<b>0.109</b>	<b>&lt;0.000001</b>
Mg	<b>0.482</b>	<b>&lt;0.000001</b>	<b>0.256</b>	<b>&lt;0.000001</b>	<b>0.122</b>	<b>&lt;0.000001</b>
K	<b>0.475</b>	<b>&lt;0.000001</b>	<b>0.212</b>	<b>&lt;0.000001</b>	<b>0.084</b>	<b>&lt;0.000001</b>

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601 Table 4. Squared Mahalanobis distances among different studied species in the discriminant functional analysis of foliar C, N, P, K, S, Ca and  
 602 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  
 603 Catalonia. All distances are significantly higher than zero based on F test ( $P < 0.001$ ).  
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A p e c i e s	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. cerrroides	Q. humilis	Q. canariensis	Q. humiliscerr
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. cerrroides																9.63	18.3	19.9
Q. humilis																	5.97	7.45
Q. canariensis																		9.53

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607 Table 5. Statistical results (Wilks' Lambda and P-value) of the discriminant function of  
 608 C, N, P, K, S, Ca and Mg concentrations and N:P, N:K and P:K concentration ratios of  
 609 leaves, branches and stems, and the foliar:wood content ratio of the seven elements  
 610 studied in the separation between angiosperms and gymnosperms, among forest groups  
 611 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	<b>0.282</b>	<b>&lt;0.000001</b>	<b>0.0857</b>	<b>&lt;0.000001</b>	<b>0.00378</b>	<b>&lt;0.000001</b>
N concentration stems	<b>0.282</b>	<b>&lt;0.000001</b>	<b>0.0799</b>	<b>&lt;0.000001</b>	<b>0.00359</b>	<b>&lt;0.000001</b>
P concentration stems	0.275	0.059	<b>0.0778</b>	<b>0.048</b>	<b>0.00337</b>	<b>0.000078</b>
S concentration stems	0.275	0.26	0.0776	0.16	0.00329	0.079
Ca concentration stems	0.275	0.10	<b>0.0801</b>	<b>&lt;0.000001</b>	<b>0.00339</b>	<b>0.000007</b>
Mg concentration stems	0.275	0.12	<b>0.0780</b>	<b>0.020</b>	<b>0.00334</b>	<b>0.00097</b>
K concentration stems	<b>0.280</b>	<b>0.000005</b>	<b>0.0798</b>	<b>0.000001</b>	<b>0.00348</b>	<b>&lt;0.000001</b>
C concentration branches	<b>0.288</b>	<b>&lt;0.000001</b>	<b>0.0888</b>	<b>&lt;0.000001</b>	<b>0.00457</b>	<b>&lt;0.000001</b>
N concentration branches	0.275	0.12	0.0774	0.30	0.00330	0.054
P concentration branches	<b>0.279</b>	<b>0.000030</b>	<b>0.0789</b>	<b>0.00013</b>	<b>0.00343</b>	<b>&lt;0.000001</b>
S concentration branches	0.274	0.73	0.0772	0.73	0.00327	0.39
Ca concentration branches	0.274	0.43	<b>0.0781</b>	<b>0.011</b>	<b>0.00335</b>	<b>0.00034</b>
Mg concentration branches	0.274	0.61	<b>0.0808</b>	<b>&lt;0.000001</b>	<b>0.00354</b>	<b>&lt;0.000001</b>
K concentration branches	<b>0.280</b>	<b>0.000004</b>	<b>0.0812</b>	<b>&lt;0.000001</b>	<b>0.00351</b>	<b>&lt;0.000001</b>
C concentration leaves	<b>0.293</b>	<b>&lt;0.000001</b>	<b>0.0922</b>	<b>&lt;0.000001</b>	<b>0.00529</b>	<b>&lt;0.000001</b>
N concentration leaves	<b>0.280</b>	<b>0.000014</b>	<b>0.0805</b>	<b>&lt;0.000001</b>	<b>0.00361</b>	<b>&lt;0.000001</b>
P concentration leaves	<b>0.281</b>	<b>0.000001</b>	<b>0.0802</b>	<b>&lt;0.000001</b>	<b>0.00342</b>	<b>&lt;0.000001</b>
S concentration leaves	0.275	0.051	<b>0.0785</b>	<b>0.0013</b>	<b>0.00345</b>	<b>&lt;0.000001</b>
Ca concentration leaves	<b>0.281</b>	<b>0.000002</b>	<b>0.0797</b>	<b>0.000001</b>	<b>0.00364</b>	<b>&lt;0.000001</b>
Mg concentration leaves	0.274	0.51	<b>0.0789</b>	<b>0.00014</b>	<b>0.00365</b>	<b>&lt;0.000001</b>
N:P leaf concentration	<b>0.282</b>	<b>&lt;0.000001</b>	<b>0.0817</b>	<b>&lt;0.000001</b>	<b>0.00344</b>	<b>&lt;0.000001</b>
N:K leaf concentration	<b>0.279</b>	<b>0.000024</b>	<b>0.0786</b>	<b>0.00069</b>	<b>0.00407</b>	<b>&lt;0.000001</b>
P:K leaf concentration	0.274	0.47	0.0776	0.14	<b>0.00345</b>	<b>&lt;0.000001</b>
N:P stems	0.274	0.37	0.0777	0.068	<b>0.00335</b>	<b>0.00032</b>
N:K stems	<b>0.280</b>	<b>0.000015</b>	<b>0.0790</b>	<b>0.000091</b>	<b>0.00338</b>	<b>0.000023</b>
P:K stems	<b>0.276</b>	<b>0.013</b>	<b>0.0781</b>	<b>0.0095</b>	<b>0.00347</b>	<b>&lt;0.000001</b>
N:P branches	0.274	0.36	<b>0.0782</b>	<b>0.0045</b>	<b>0.00340</b>	<b>0.000002</b>
N:K branches	0.275	0.093	0.0777	0.072	<b>0.00332</b>	<b>0.011</b>
P:K branches	<b>0.282</b>	<b>&lt;0.000001</b>	<b>0.0800</b>	<b>&lt;0.000001</b>	<b>0.00332</b>	<b>0.013</b>
C (L/W) content ratio	<b>0.275</b>	<b>0.039</b>	<b>0.0861</b>	<b>&lt;0.000001</b>	<b>0.00347</b>	<b>&lt;0.000001</b>
N(L/W) content ratio	0.275	0.071	0.0775	0.26	<b>0.00374</b>	<b>&lt;0.000001</b>
P(L/W) content ratio	<b>0.277</b>	<b>0.0017</b>	<b>0.0778</b>	<b>0.039</b>	<b>0.00335</b>	<b>0.00063</b>
S(L/W) content ratio	0.275	0.24	0.0776	0.15	<b>0.00341</b>	<b>0.000001</b>
Ca(L/W) content ratio	<b>0.277</b>	<b>0.00079</b>	<b>0.0851</b>	<b>&lt;0.000001</b>	<b>0.00349</b>	<b>&lt;0.000001</b>
Mg(L/W) content ratio	0.274	0.41	<b>0.0802</b>	<b>&lt;0.000001</b>	<b>0.00378</b>	<b>&lt;0.000001</b>
K(L/W) content ratio	<b>0.275</b>	<b>0.039</b>	<b>0.0783</b>	<b>0.0029</b>	<b>0.00395</b>	<b>&lt;0.000001</b>

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625 Table 6. Test statistics for squared Mahalanobis distances among different forest groups  
 626 in the discriminant functional analysis with C, N, P, K, S, Ca and Mg concentrations  
 627 and N:P, N:K and P:K concentration ratios of leaves, branches and stems, and the  
 628 foliar:wood content ratio of the seven elements studied as variables and the 1004 plots  
 629 dominated by the 15 most representative forest tree species of Catalonia. All distances  
 630 are significantly higher than zero based on F test ( $P < 0.001$ ).  
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Ecotype groups	Transition Med-temp	Wet temp. angiosperms	Med gymnosperms	Alpine gymnosperms
Med. Angiosperms evergreens	<b>9.90</b>	<b>24.1</b>	<b>12.5</b>	<b>15.5</b>
Transition Med-temp		<b>22.5</b>	<b>14.2</b>	<b>15.9</b>
Wet temp. angiosperms			<b>31.3</b>	<b>27.5</b>
Med gymnosperms				<b>3.47</b>

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665 Table 7. Test statistics for squared Mahalanobis distances among different studied species in the discriminant functional analysis with C, N, P, K,  
 666 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  
 667 seven elements studied as variables and the 1004 plots dominated by the 15 most representative forest tree species of Catalonia. All distances are  
 668 significantly higher than zero based on F test ( $P < 0.001$ ).

	<i>Pinus sylvestris</i>	<i>Pinus nigra</i>	<i>Pinus uncinata</i>	<i>Pinus pinaster</i>	<i>Quercus ilex</i>	<i>Pinus pinea</i>	<i>Castanea sativa</i>	<i>Arbutus unedo</i>	<i>Quercus canariensis x humilis</i>	<i>Quercus suber</i>	<i>Quercus cerrioides</i>	<i>Quercus humilis</i>	<i>Quercus petraea</i>	<i>Fagus sylvatica</i>
<i>Pinus halepensis</i>	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
<i>Pinus sylvestris</i>		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
<i>Pinus nigra</i>			13.8	19.6	21.7	19.7	42.0	22.4	21.2	36.20	89.2	26.5	44.5	42.1
<i>Pinus uncinata</i>				29.8	50.3	55.5	68.2	51.8	47.2	61.5	115	54.2	78.7	72.9
<i>Pinus pinaster</i>					26.3	37.0	40.1	39.8	32.4	43.7	88.4	36.8	64.5	58.7
<i>Quercus ilex</i>						23.9	39.8	13.23	9.89	18.6	60.4	13.8	32.4	30.1
<i>Pinus pinea</i>							49.8	20.1	27.7	42.9	86.6	29.2	45.0	42.6
<i>Castanea sativa</i>								39.2	26.5	54.7	108	42.2	46.9	48.6
<i>Arbutus unedo</i>									14.1	32.7	80.4	19.3	33.5	36.4
<i>Quercus canariensis x humilis</i>										20.0	60.3	11.5	28.0	31.9
<i>Quercus suber</i>											68.0	23.0	38.5	35.49
<i>Quercus cerrioides</i>												50.5	95.5	86.09
<i>Quercus humilis</i>													24.0	30.6
<i>Quercus petraea</i>														16.0

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675 **Figure captions**

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

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

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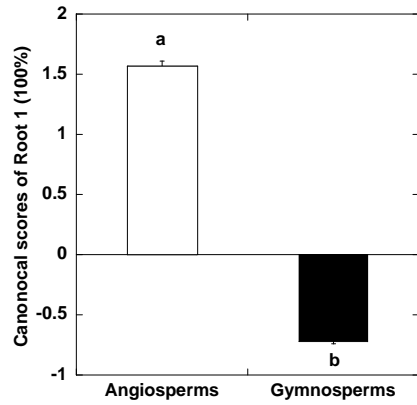
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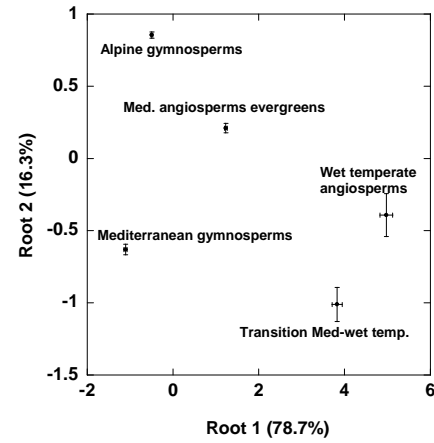
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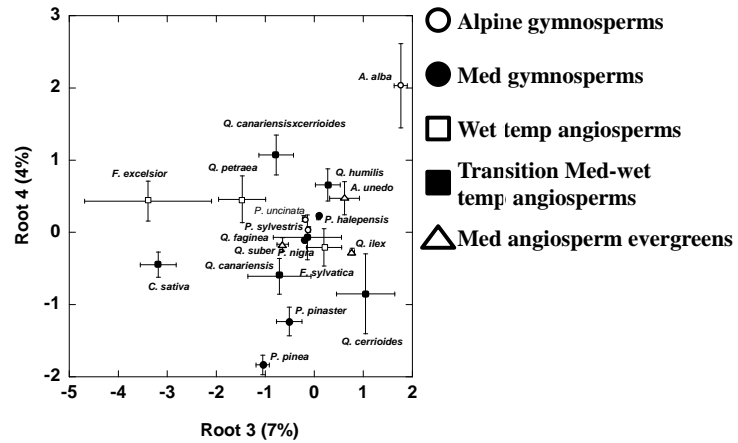
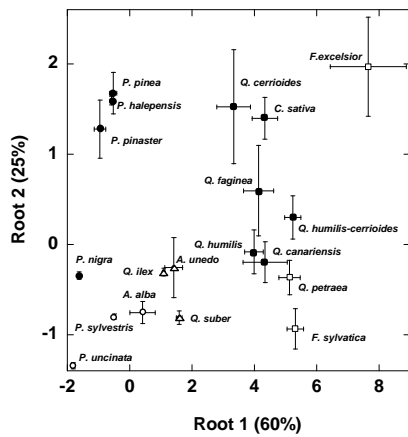
**A** Separation between angiosperms and gymnosperms



**B** Separation among forest types



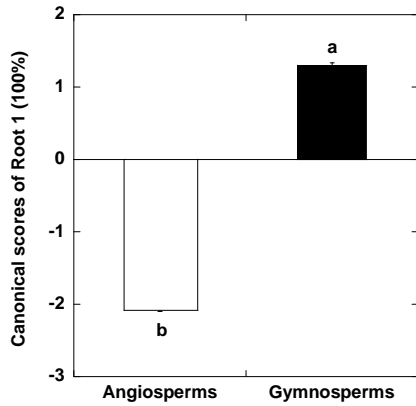
**C** Separation among species



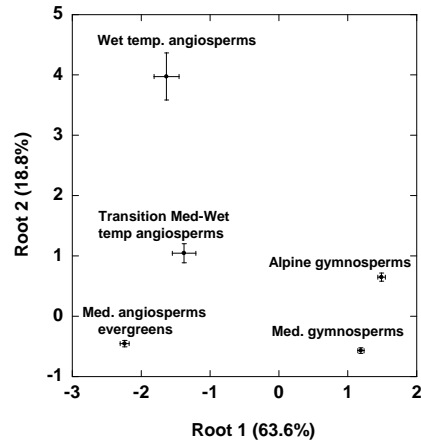
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702 Figure 1

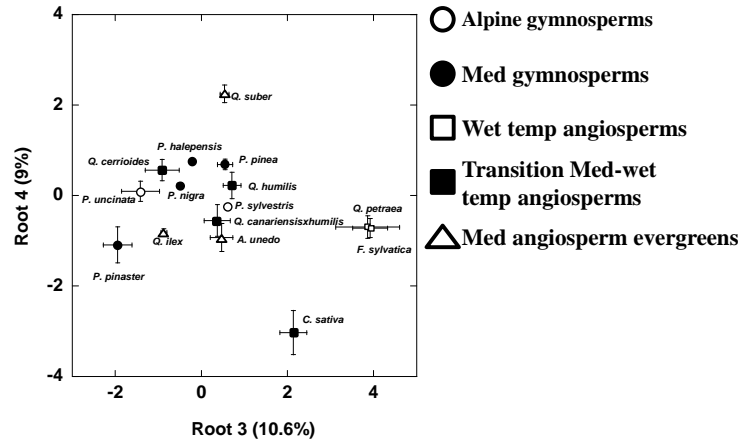
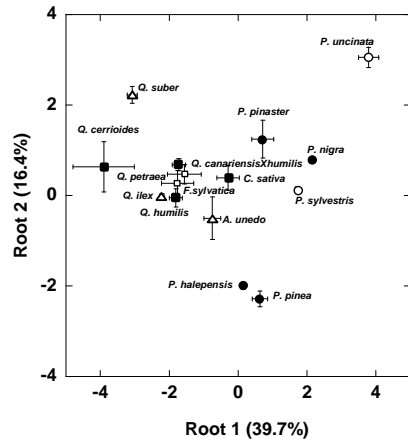
**A** Separation between angiosperms and gymnosperms



**B** Separation among forsts types



**C** Separation among species



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704 Figure 2