

1 Title: Tree species effects on nutrient cycling and soil biota: a feedback mechanism favouring
2 species coexistence.

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13 ABSTRACT

14 We synthesize a series of independent but integrated studies on the functioning of a mixed
15 Mediterranean oak forest to demonstrate the tree-soil interactions underpinning a positive
16 feedback process that sustains the coexistence of two oak species. The studies focused on the
17 foliar functional traits, plant regeneration patterns, biogeochemical cycles, soil microbial
18 biomass and ectomycorrhizal (ECM) fungal diversity associated with the co-dominant evergreen
19 *Quercus suber* and deciduous *Q. canariensis* in a Mediterranean forest in southern Spain.

20 Foliar attributes differed between oak species, with *Q. canariensis* having higher nutrient content
21 and lower carbon to nutrient ratios and leaf mass per area than *Q. suber*. These attributes
22 reflected their distinct resource use strategies and adaptation to high and low resource-
23 availability environments, respectively. Leaf-fall nutrient concentrations were higher in *Q.*
24 *canariensis* than in *Q. suber* and were correlated with concentrations in the fresh leaves. Leaf-
25 fall nutrient concentrations influenced nutrient return, leaf-fall decay rate and the proportion of
26 nutrients released from decomposing leaf-fall, all of which were higher for *Q. canariensis* than
27 for *Q. suber*. This generated a differential net nutrient input into the soil that led to increased soil
28 nutrient concentrations under the canopy of *Q. canariensis* as compared to *Q. suber*. The fraction
29 of slowly decomposing leaf-fall that builds up soil organic matter was higher for *Q. canariensis*,
30 further raising the nutrient and moisture retention of its soils. Differences between species in soil
31 properties disappeared with increasing soil depth, which was consistent with the hypothesised
32 leaf-fall-mediated effect. Tree-species-generated changes in soil properties had further impacts
33 on soil organisms. Soil microbial biomass (C_{mic}) and nutrients (N_{mic}, P_{mic}) were higher under
34 *Q. canariensis* than under *Q. suber* and were positively related to soil moisture content and
35 substrate availability (particularly soil N). The composition of the ECM fungal community
36 shifted between the two oaks in response to changes in the soil properties, particularly soil Ca
37 and pH. Lower ECM phylogenetic diversity and higher abundance of mycorrhizal species with
38 saprophytic abilities were related to the greater soil fertility under *Q. canariensis*. Overall, the
39 two oak species generated soil conditions that aligned with their resource-use strategies and
40 would enhance their own competitive capabilities, potentially creating a positive feedback. The
41 two *Quercus* created soil spatial heterogeneity that could enable their coexistence through spatial

42 niche partitioning. This study demonstrates the critical role of aboveground-belowground
43 interactions underpinning forest community composition.

44 Keywords

45 feedback processes, microbial biomass, mycorrhizal fungi, nutrient cycling, plant-soil

46 interactions, *Quercus*

47

48 1. INTRODUCTION

49 Plant species coexistence has always intrigued ecologists, particularly in relation to
50 environmental variability (Grime, 1979; Tilman, 1988). Recently a call has been made to
51 move from describing patterns to understanding the mechanisms driving coexistence
52 (Agrawal *et al.*, 2007). As a result there has been a rapid increase in the number of studies
53 suggesting that aboveground and belowground processes, and particularly plant-soil
54 feedbacks, are among the main mechanisms underpinning species abundance, coexistence
55 and succession (Kardol *et al.*, 2006; Kulmatiski *et al.*, 2008; Miki *et al.*, 2010; van der Putten
56 *et al.*, 2013).

57 Plant-soil feedbacks occur whenever a plant causes species-specific changes to soil biotic or
58 abiotic properties that in turn affect the establishment, growth or reproduction of their own
59 species (Bever, 1994; Ehrenfeld *et al.*, 2005). Both positive and negative feedbacks can
60 promote coexistence: negative feedbacks diminish the fitness differences between species *via*
61 equalising mechanisms (*sensu* (Barot, 2004) leading to dynamic coexistence whereas positive
62 feedbacks generate multiple steady states and promote coexistence *via* space and/or time
63 partitioning (Pacala and Levin, 1997; Barot, 2004). In both cases the underlying mechanisms
64 rely on the ability of the species to generate environmental conditions that alter competitive
65 interactions and facilitate or prevent other species establishment.

66 Many studies have shown that trees are ecosystem engineers able to generate species-specific
67 effects on soil properties and soil communities that could potentially lead to a feedback effect
68 (Gómez-Aparicio and Canham, 2008; Vesterdal *et al.*, 2008; Mitchell *et al.*, 2012; Vesterdal
69 *et al.*, 2012; Prescott and Grayston, 2013 and references therein). However, few of them have
70 investigated the processes underpinning those effects and their consequences for ecosystem
71 properties (Reich *et al.*, 2005; Mitchell *et al.*, 2007; Ayres *et al.*, 2009). Furthermore, these
72 studies are often focused on a particular aspect of tree-soil interactions. For instance, studies
73 have separately addressed tree species effect on light availability, soil chemical properties,
74 decomposer community or the effects of soils on species distributions (Canham *et al.*, 1994;
75 Van Breemen *et al.*, 1997; Hobbie *et al.*, 2006; Turk *et al.*, 2008). To our knowledge only a
76 few studies have presented a holistic vision of the multiple concomitant tree-soil interaction
77 processes occurring at a single site despite its importance to ecosystem functioning (Ayres *et*
78 *al.*, 2009). Thus a major effort is needed to integrate the current knowledge on the multiple

79 functional processes and ecological mechanisms that underpin ecosystems` composition and
80 dynamics.

81 To address this knowledge gap we bring together a series of independent but integrated
82 studies on the functioning of a mixed Mediterranean forest ecosystem. The studies
83 investigated the effects of the coexisting evergreen *Quercus suber* and the winter deciduous
84 *Q. canariensis* on different ecosystem properties. In particular they characterized the foliar
85 traits of both oak species (Domínguez *et al.*, 2012) and addressed species effects on nutrient
86 cycling (Aponte *et al.*, 2011), litter decomposition (Aponte *et al.*, 2012), and soil biota
87 (Aponte *et al.*, 2010a; Aponte *et al.*, 2010b). The aim of this synthesis is to review the results
88 of these studies and to discuss whether these interactions could sustain a feedback mechanism
89 driving the coexistence of the two *Quercus* species.

90 Our overarching hypothesis is that the two oak species, through differences in their leaf-fall
91 nutrient concentration, generate species-specific changes in the soil abiotic properties that
92 further affect the soil biota and that could ultimately increase their own fitness. To that end
93 we sequentially examined the following hypotheses: 1) *Q. canariensis* has higher leaf
94 nutrient content and different morphological traits than *Q. suber*, which reflect their different
95 ecological strategies; 2) The attributes of the fresh leaves are inherited by the leaf-fall,
96 resulting in *Q. canariensis* having higher leaf-fall quality and nutrient return than *Q. suber*; 3)
97 Higher leaf-fall quality leads to higher decomposition rate and nutrient release into soil; 4)
98 The higher nutrient return and release from *Q. canariensis* leaf-fall increases its soil fertility
99 levels as compared to *Q. suber*; 5) Species-induced changes in soil nutrient content affect the
100 size and properties of the soil microbial biomass and alter the species community
101 composition of the ectomycorrhizal fungal community; 6) Tree species generate a soil
102 environment where their competitive abilities are enhanced, thus increasing their fitness and
103 leading to a positive feedback. At a stand scale, this creates a mosaic of soil conditions that
104 allows for a spatial niche separation and sustains their coexistence.

105

106 2. MATERIALS AND METHODS

107 2.1. Study area

108 The studies were conducted in a mixed oak forest located in southern Spain, near the Strait of
109 Gibraltar. This area of about 1000 km² holds high ecological value. The rough relief and
110 acidic nutrient-poor soils, which made the area unsuitable for cultivation, its frontier location,
111 which limited deforestation and settlement during medieval times, and the rise of the value of
112 the cork harvested from the *Q. suber* have contributed to the ecological maintenance of this
113 area now protected as “Los Alcornocales” (meaning the cork oak woodlands) Natural Park
114 (Marañón and Ojeda, 1998).

115 The forest grows on Oligo-Miocene sandstone bedrock that is interspersed with layers of
116 marl sediments. The area has sub-humid Mediterranean climate, the annual mean temperature
117 is 16.5 °C and the annual rainfall ranges from 701 to 1331 mm (Anonymous, 2005). Two oak
118 species coexist in the area distributed along a topographic gradient: the evergreen *Quercus*
119 *suber* dominates on the nutrient-poor soils on the ridges whereas the deciduous *Q.*
120 *canariensis* dominates at the valley bottoms. Both species co-dominate in mixed stands on
121 the midslope (Urbieto *et al.*, 2008).

122 The studies were conducted in two 1-ha mixed forest stands located on the midslope of two
123 forest sites (30km apart) named San Carlos del Tiradero (36°9'46"N, 5°35'39"W) and La
124 Saucedá (36°31'54"N, 5°34'29"W). The stand in Tiradero (335-360 m a.s.l) had a higher
125 density of trees (768 stems ha⁻¹) and a close canopy (LAI 2.26 m² m⁻²) compared to La
126 Saucedá (530-560 m a.s.l; 219 stems ha⁻¹; LAI 1.84 m² m⁻²). Soils in Tiradero had similar
127 carbon content (3.13 % vs. 3.27%), C/N ratios (15.6 vs. 16.1) and pH (4.0 vs. 4.8) but higher
128 sand content (58% vs. 47%) than those in La Saucedá (mean values over the first 50 cm). At
129 each 1-ha stand ten individuals of the evergreen *Q. suber* and ten individuals of the deciduous
130 *Q. canariensis* were selected. The selected trees in the mixed forest stands had their nearest
131 hetero-specific neighbour within approximately 4 to 10 m.

132 2.2. Methods

133 This study draw upon several datasets gathered over more than five years of studies in the
134 above-mentioned forest stands (Tiradero and La Saucedá). Some of these datasets had been
135 separately analysed to address specific questions on plant functional traits, litter
136 decomposition or soil heterogeneity among others and the results have been previously
137 published (Aponte *et al.*, 2010a; Aponte *et al.*, 2010b; Aponte *et al.*, 2011; Aponte *et al.*,
138 2012; Domínguez *et al.*, 2012). Other datasets had remained unpublished. Here we reviewed

139 the results of these studies and reanalysed the combined datasets to obtain an integrated view
140 of the ecosystem functioning.

141 Leaf traits, including four morphological and 19 chemical traits were analysed in 17 woody
142 plant species (including both oak species) from the forest community in La Saucedá. Leaf
143 mass per area (LMA, g m^{-2}) and leaf dry matter content (LDMC, g g^{-1}) were measured
144 following methods in Cornelissen *et al.* (2003). Leaf carbon concentration was determined in
145 an elemental analyser (CHNS Eurovector EA-3000). Nitrogen was analysed by Kjeldahl
146 digestion (Jones and Case, 1990). Leaf macronutrients (Ca, K, Mg, P, and S) and
147 micronutrients (Cu, Co, Fe, Mn, Ni and Zn) concentrations were determined by acid
148 digestion followed by ICP-OES analysis. Isotopic analyses of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) in leaf
149 samples were performed using a continuous-flow elemental analyser – isotopic-ratio mass
150 spectrometer (EA Thermo 1112-IRMS Thermo Delta V Advantage). For more details on leaf
151 trait analysis see Domínguez *et al.* (2012).

152 Tree species nutrient return and effects on soil fertility were examined for the 40 selected oak
153 trees. Fresh leaves, leaf-fall, litter, topsoil (0–25 cm depth) and subsoil (25–50cm depth),
154 were sampled in November 2006. Leaf-fall, litter and soil were sampled beneath the canopy
155 of each selected oak. Accumulated annual leaf-fall was collected in four traps under each
156 tree. Litter was considered dead plant material relatively undecomposed standing on the
157 ground and it was harvested within two 30 x 30 cm quadrats. Soil cores were extracted with a
158 cylindrical auger after removing the litter layer. Soil pH was determined in a 1:2.5 soil:CaCl
159 0.01M solution. Soil carbon was estimated using a total organic carbon analyser (TOCVesh),
160 available soil P was estimated using the Bray-Kurtz method and soil NH_4^+ was estimated by
161 extraction with KCl (2M) and steam distillation. Total concentration of several nutrients (Ca,
162 K, Mg, P, S, Mn, Cu and Zn) in plant tissues and soils was determined using wet oxidation
163 with HNO_3 (for plants) or $\text{HCl} + \text{HNO}_3$ (for soils) under pressure in a microwave digester
164 followed by ICP- OES analysis. Plant and soil N was determined by Kjeldahl digestion.
165 Further details on the methods can be found in Aponte *et al.* (2011).

166 Leaf-fall decay and nutrient release were examined using a litterbag decomposition
167 experiment. Litterbags containing freshly senesced leaves from *Q. suber* or *Q. canariensis*
168 were incubated beneath the canopies of the selected oak trees, beneath shrubby cover and in
169 open areas. Litterbags were harvested every 6 months for 2 years. Upon harvest, leaf litter
170 was removed from the bags, dried and weighed for mass loss. Samples were ground and

171 analysed for C, N, Ca, K, Mg, P, S, Mn, Cu and Zn to assess changes in nutrient content over
172 time. Biomass loss (in this case carbon loss) was fitted with an asymptotic model, $M_t = m +$
173 $(1 - m)e^{-kt}$, where M_t was the proportion of remaining mass at time t , m was the fraction of
174 the initial mass with a decomposition rate of zero (that is, the asymptote) and k was the
175 decomposition rate of the remaining fraction $(1 - m)$. The asymptotic model implied that
176 there was a limit value (m) for mass loss. This value corresponded to a very stable fraction of
177 the litter that decomposed extremely slow over the time span of the experiment (Berg *et al.*,
178 2003). See further methodological details in Aponte *et al.* (2012).

179 Soil microbial C, N and P content were estimated on soil samples extracted at two depths (0–
180 8 cm and 8–16 cm after removing the litter layer) beneath the selected oak trees. Soil
181 samples were taken in spring (May–June), summer (September) and autumn (December)
182 2007, and spring (May) 2008. Microbial C, N and P were estimated using a chloroform
183 fumigation-extraction procedure (Brookes *et al.*, 1982; Brookes *et al.*, 1985; Vance *et al.*,
184 1987). Two soil subsamples were extracted using 0.5 M K_2SO_4 or 0.025 N HCl + 0.03 N
185 NH_4F for subsequent determination of microbial C and N or microbial P, respectively. Other
186 two soil subsamples were fumigated with chloroform for 24 h in a vacuum desiccator,
187 followed by the same extraction procedure as the unfumigated samples. Carbon and N in
188 fumigated and unfumigated soil extracts were determined using a Total Dissolved Organic
189 Carbon and Nitrogen Analyzer (TOC-Vesh). Microbial C and N were estimated as the
190 difference in K_2SO_4 -extractable dissolved organic carbon or nitrogen between fumigated and
191 unfumigated soils using as extractability correction factors: $K_C = 0.45$ for C and $K_N = 0.40$
192 for N (Jonasson *et al.*, 1996). Available P in NH_4F soil extracts was measured using the
193 Bray-Kurtz method (Bray and Kurtz, 1945). Microbial P was estimated as the difference in
194 available P between fumigated and unfumigated soil using a correction factor $K_P = 0.40$
195 (Brookes *et al.*, 1982). For more methodological details see Aponte *et al.* (2010b).

196 The community composition of the ectomycorrhizal fungi associated with the roots of the
197 selected oak trees was identified using PCR-based molecular method. Superficial roots (15
198 cm depth) approximately equal in length (20 cm) were taken from each selected tree, close to
199 the litter and soil sampling points, in November 2007. From each tree 20 mycorrhizal root
200 tips were randomly picked. Mycorrhizal DNA was extracted using the Wizard Genomic
201 DNA Purification Kit (Promega, Charbonnieres, France) and the internal transcribed spacer
202 regions I and II and the nuclear 5.8S rRNA gene were amplified using the primer sets ITS-

203 1F/ITS-4B (Gardes and Bruns, 1993) or ITS-1F/ITS-4 (White *et al.*, 1990). The sequencing
204 of the final amplification products was done by MilleGen (Labège, France). Ectomycorrhizal
205 species (“Operational taxonomic units” *sensu* (Blaxter *et al.*, 2005) were determined by
206 BLAST searches against GenBank and the UNITE database. See methodological details in
207 Aponte *et al.* (2010a).

208 2.3. Data analysis

209 A range of multivariate ordination techniques, namely Principal Component Analysis (PCA),
210 Canonical Correspondence Analysis (CCA) and path analysis, were used to better understand
211 the multivariate patterns present in the data. Principal Component Analysis was applied to
212 single tables to explore the variability within datasets. Canonical Correspondence Analysis
213 was used to analyse the relationship between the ECM community composition and
214 environmental conditions. Path analysis with d-sep tests was used to evaluate alternative
215 causal relationships among the properties of the ecosystem components (Shipley, 2000).
216 Differences between *Quercus* species in the univariate or multivariate space were evaluated
217 using Analysis of Variance (ANOVA) or Mann-Witney non-parametric test for small sample
218 sizes.

219

220 3. RESULTS AND DISCUSSION

221 3.1. Leaf traits

222 The traits of the fresh leaves of *Q. canariensis* and *Q. suber*, together with other 15 woody
223 species of the plant community in La Saucedá, were studied by Domínguez *et al.* (2012)
224 using a principal component analysis (Fig 1, a). The first PCA axis accounted for 26% of the
225 variability of the traits attributes and it was negatively related to leaf nutrient concentration
226 and positively related to leaf mass per area (LMA), leaf dry matter content (LDMC), carbon
227 concentration, δC^{13} and carbon to nitrogen ratio. We analysed the differences between the
228 two *Quercus* in the multivariate space defined by the PCA and observed that the two species
229 had significantly different scores along the first axis (Mann-Whitney U test, n=10
230 individuals, $P < 0.009$): the evergreen *Q. suber* grouped with other sclerophyllous species at
231 the positive end of the first axis, whereas *Q. canariensis* was on the negative side of the same
232 axis (Fig 1, a). Similar results were obtained when we analysed the attributes of the fresh
233 leaves sampled from the 40 oak trees (20 *Q. suber* and 20 *Q. canariensis*) in the two forest

234 sites (La Saucedá and Tiradero; Fig 1, b); the first PCA axis accounted for 36% of the
235 variability of the dataset and clearly separated the two *Quercus* species ($P < 0.001$). Both
236 analyses indicated that *Q. suber* had a higher LMA, LDMC, C, C:N and δC^{13} and lower
237 nutrient concentrations than *Q. canariensis*.

238 Species leaf trait values reflect their functional strategy to manage resources such as water,
239 light and nutrients (Poorter *et al.*, 2009; Pérez-Ramos *et al.*, 2012). Two main opposite
240 strategies can be distinguished from the global range of traits variation that defines the *leaf*
241 *economics spectrum* (Wright *et al.*, 2004): a conservative resource-use strategy and resource-
242 acquisition strategy. The first one is defined by slow rates of resource acquisition and
243 minimum resource loss and it is characteristic of species adapted to resource-limited
244 environment, whereas the opposite is true for the second one (Aerts, 1995). The differences
245 in the foliar attributes of the studied oaks align each species with one of the divergent
246 ecological strategies. That is, *Q. suber* could be considered to have a conservative-resource
247 strategy because of its higher values of LMA, higher density tissues, higher efficiency in the
248 use of water (high C^{13} (Farquhar *et al.*, 1989)) and higher carbon-to-nutrient ratios. In
249 contrast *Q. canariensis*, which exhibited opposite attributes, would be ascribed to the
250 resource-acquisition strategy (Wright *et al.*, 2005; Villar *et al.*, 2006). The divergence in
251 their strategies is consistent with their distinct decomposability (lower for *Q. suber*), which
252 would lead to slower nutrient loss during decomposition (Gallardo and Merino, 1993; Aponte
253 *et al.*, 2012).

254 Species resource-use strategies are the result of their adaptive evolution to environmental
255 conditions (Reich *et al.*, 2003), which suggests that the two *Quercus* would be adapted to
256 environments with distinct resource (water, light and nutrients) availability. This was
257 sustained by Urbietta *et al.* (2008) who examined the dominance of both oak species along a
258 topographic gradient in a 284-ha mixed forest stand within Los Alcornocales National Park.
259 They observed that the abundance of *Q. suber* increased with altitude and distance from the
260 valley bottom (i.e., decreasing water and nutrient availability) whereas the opposite was
261 observed for *Q. canariensis*. Higher water availability also increased seedling performance
262 and survival rate of *Q. canariensis* but did not affect *Q. suber* in greenhouse and field
263 experiments (Quero *et al.*, 2006; Pérez-Ramos, 2007). Studies on the regeneration of both
264 oak species demonstrated that in low-light environments (i.e., dense plant cover, high litter
265 depth and nutrient availability) *Q. canariensis* had higher survival and growth rate than *Q.*

266 *suber*. However in high-light, nutrient-poor environments the evergreen *Q. suber* seedlings
267 outgrew the deciduous species (García *et al.*, 2006; Gómez-Aparicio *et al.*, 2008b; Pérez-
268 Ramos *et al.*, 2010). The differential response of *Q. canariensis* and *Q. suber* to resource
269 availability suggests that their coexistence might be mediated through niche partitioning.

270 Species leaf attributes are not only a response to environmental conditions but also determine
271 species effect on the ecosystem properties (Diaz *et al.*, 2004; Ayres *et al.*, 2009). For
272 instance, the chemical and morphological attributes of fresh leaves and senesced leaves (leaf-
273 fall) influence soil nutrient availability through its effects on biogeochemical processes (e.g.,
274 nutrient throughfall, decomposition) (Facelli and Pickett, 1991; Prescott, 2002; Hobbie *et al.*,
275 2006). Therefore the distinct foliar attributes of the studies species would likely generate
276 contrasting effects on the ecosystem properties.

277 3.2. Leaf-fall and nutrient return

278 The nutrient concentration of the fresh leaves and leaf-fall of the 40 oak trees in the two
279 forest sites was highly correlated (Aponte *et al.*, 2011), resulting in *Q. canariensis* having
280 higher leaf litter quality than *Q. suber* (Fig 2). This was consistent with results from the leaf-
281 fall decomposition study by Aponte *et al.* (2012), who reported higher concentrations of N,
282 Ca, Mg, P and S ($P < 0.001$) in the leaf-fall of *Q. canariensis* as compared to *Q. suber*.
283 Differences between species were particularly high for macronutrients such as Ca (51%
284 higher in *Q. canariensis* leaf-fall), P (28%) and Mg (26%). These results indicate that fresh
285 leaf attributes, and thus differences between species, were inherited by the leaf-fall. However,
286 the relationship between fresh leaf and leaf-fall mineral content cannot be generalised since
287 leaf-fall nutrient content might be influenced by nutrient resorption during the senescing
288 process (Aerts, 1996). Nutrient resorption minimizes nutrient losses and therefore high
289 resorption efficiency would be expected from species exhibiting a conservative use of
290 resources. Conversely, in our study *Q. suber* and *Q. canariensis* did not differ in proportional
291 resorption of N (39% *Q. canariensis* vs. 36% *Q. suber*) or P (39.7% *Q. canariensis* vs. 41%
292 *Q. suber*). Other nutrients measured (Ca, Mg, S, Mn, Cu, Fe, Zn) were not resorbed but
293 instead accumulated in the leaf-fall. Aerts *et al.* (1996) also observed small (47% vs. 54%) or
294 no differences in the resorption of N and P between evergreen and deciduous trees and
295 concluded that the lower nutrient concentration in evergreen leaf-fall contributed more to
296 nutrient conservation than did nutrient resorption.

297 Annual leaf-fall production of *Q. canariensis* and *Q. suber* was similar in amount (0.30 and
298 0.29 kg/m² respectively). Comparable leaf-fall production values were found for the winter
299 deciduous *Q. pyrenaica* (0.237 kg/m²) in the centre of Spain (Salamanca), and the evergreens
300 *Q. lanuginose* (0.246 kg/m²) and *Q. ilex* (0.243 kg/m²) in the south of France (Montpellier)
301 (Rapp *et al.*, 1999), suggesting that, at least for this genus, leaf-fall productivity is not
302 necessarily related to foliar habit. Both leaf-fall nutrient content and leaf-fall quantity
303 determine tree species nutrient return and their impact on ecosystem properties (Facelli and
304 Pickett, 1991; Washburn and Arthur, 2003). Leaf-fall quantity could be more influential than
305 quality in terms of net nutrient return to soil if the different masses of leaf-fall overrode the
306 differences in nutrient concentrations (Chabot, 1982; Cuevas and Lugo, 1998). However this
307 was not the case for *Q. suber* and *Q. canariensis*, which had comparable leaf-fall production.
308 Therefore the nutrient concentration of the leaf-fall created the distinct nutrient return of the
309 two species.

310 3.3. Leaf-fall decomposition and nutrient release

311 Leaf-fall decomposition of *Q. suber* and *Q. canariensis* were measured in a two-year litterbag
312 experiment (Aponte *et al.* 2012). During the early stages of decomposition leaf-fall of *Q.*
313 *canariensis* had higher chemical quality, particularly the higher concentrations of N (lower
314 C:N) and Ca, and decayed faster than that of *Q. suber*. Leaf-fall quality largely controls leaf
315 litter decomposition and release of nutrients into soil and thus could potentially explain
316 species effects on soil fertility (Norris *et al.*, 2012). High leaf-fall quality has been related to
317 high nutrient content and low carbon to nutrient ratios but also to low non-structural and
318 recalcitrant carbohydrate concentrations (e.g. lignin, tannins, phenolic) and low leaf mass per
319 area and foliar toughness (Gallardo and Merino, 1993; Pérez-Harguindeguy *et al.*, 2000;
320 Aerts *et al.*, 2003; Hättenschwiler and Jørgensen, 2010). Most of these properties differed
321 between *Q. suber* and *Q. canariensis* in keeping with their distinct decay rates (Gallardo and
322 Merino, 1993).

323 In contrast to the pattern observed during early decomposition, the limit value of
324 decomposition, i.e. the fraction of leaf litter mass that remains stable at late stages of
325 decomposition and builds up soil organic matter, was higher for *Q. canariensis* than for *Q.*
326 *suber* (40% vs. 31%, $p < 0.0001$; Aponte *et al.* 2012). This was consistent with the larger
327 concentrations of soil organic matter measured under the canopy of *Q. canariensis* than under
328 *Q. suber* (Aponte *et al.*, 2010b; Aponte *et al.*, 2011). Differences in species limit value were

329 related to their distinct N, Ca and Mn content. Nitrogen and Ca, which enhanced early decay
330 rates, hindered late stage decomposition, thus exerting counteracting effects over time. In
331 high-N substrates microbes are not N-limited and have higher substrate use efficiency. This
332 results in a faster initial decomposition but also in a greater accumulation of microbial
333 products and residues over the long term. These microbial products, when bonded with metal
334 polyvalent cation such as Ca, are the precursors of stable SOM formation (Davey *et al.*, 2007;
335 Cotrufo *et al.*, 2013). Manganese was the only nutrient which concentration was higher in *Q.*
336 *suber* than in *Q. canariensis* leaf-fall and it emerged as the most important driver of carbon
337 loss during late decomposition. The effect of Mn was related to its role as a cofactor in a
338 lignin degrading enzyme (Eriksson *et al.*, 1990; Davey *et al.*, 2007).

339 Aponte *et al.* (2012) also observed that the rate and proportion of nutrients loss from
340 decomposing leaf-fall was higher for *Q. canariensis* than for *Q. suber*. For example, after 6
341 months *Q. canariensis* leaf-fall had lost 49% and 17% of its P and N content respectively. In
342 contrast *Q. suber* had lost 29% of its P content and none of its N. The species differences in
343 their relative nutrient loss during decomposition added to the differences in species nutrient
344 return. As a result, *Q. canariensis* released a higher net amount of nutrients into the soil than
345 *Q. suber* (Fig 3). For instance, after two years *Q. canariensis* would have released 12 kg ha⁻¹
346 of N (31% of the initial input), 8.6 kg ha⁻¹ of Ca (19%) and 2.1 kg ha⁻¹ of P (67%) whereas *Q.*
347 *suber* would have released 2.1 kg ha⁻¹ of N (8%), 3.1 kg ha⁻¹ of Ca (11%) and 0.9 kg ha⁻¹ of P
348 (50%). Nutrient return from *Q. canariensis* could have been slightly higher since, due to its
349 marcescent habit, a fraction of the soluble nutrients in its leaf-fall could have been leached
350 over the winter before our sampling (Ibrahima *et al.*, 1995). Nevertheless this would further
351 increase the differences in nutrient release between oak species.

352 Leaf-fall decomposition is not only influenced by its quality it can also be affected by the soil
353 biota and environmental conditions (i.e., moisture, UV radiation, temperature (Hobbie, 1996;
354 Austin and Vivanco, 2006; Negrete-Yankelevich *et al.*, 2008). Aponte *et al.* (2012) evaluated
355 the relative importance of substrate (leaf-fall) quality *versus* tree-generated environmental
356 conditions on the decomposition of *Q. suber* and *Q. canariensis* leaf-fall by incubating
357 litterbags beneath the canopies of both species. Leaf-fall quality explained a greater
358 percentage of the variation of early and late decay parameters (35.2% and 19.6 %
359 respectively) than topsoil environmental conditions (4.4% and 4.5%). Nevertheless, the
360 higher moisture content and higher N and P concentration of the soils beneath *Q. canariensis*

361 positively influenced leaf-fall decay of both species. These results are in accordance with
362 other studies that suggest that long term tree-soil interactions can shape topsoil properties and
363 organisms thus allowing for a potential indirect effect of trees species on leaf-fall decay *via*
364 changes in soil environment (Mitchell *et al.*, 2007; Vivanco and Austin, 2008; Freschet *et al.*,
365 2012). For instance, Reich *et al.* (2005) and Hobbie *et al.*(2006) showed that tree species
366 affected leaf-fall decomposition through variation in leaf-fall quality, soil temperature and
367 earthworm community. Chadwick *et al.* (1998) observed that leaf-fall decay rate was
368 influenced by the nutrient content of the layer of litter on which leaf-fall was incubated.
369 Recently Vesterdal *et al.* (2012) correlated the leaf-fall quality (N, Ca and Mg) and
370 microclimatic conditions generated by five deciduous tree species with forest floor C
371 turnover rates.

372 Overall, the distinct nutrient return and decay patterns of both *Quercus* species, controlled by
373 their leaf-fall quality, resulted in a differential nutrient input into the soils that could in turn
374 alter soil nutrient availability. In addition, the higher limit value of decomposition of *Q.*
375 *canariensis* lead to higher levels of SOM and thus higher retention of nutrients and moisture,
376 further reinforcing the ability of *Q. canariensis* to change soil conditions.

377 3.4. Soil nutrient content

378 We analysed the chemical and textural characteristics of the subsoil (25-50 cm) sampled
379 beneath the 40 *Q. canariensis* and *Q. suber* trees within each forest site as a proxy of the
380 original soil conditions. No differences were found between the two species (Supplementary
381 figure S2), suggesting that the parent material i.e. the original soil conditions, within stands
382 was homogeneous. In contrast, topsoil (0-25 cm) carbon and nutrient concentration and pH
383 were significantly ($P<0.05$) higher under *Q. canariensis* than under *Q. suber*, consistent with
384 the differences in nutrient return and decomposition dynamics. The multivariate analysis of
385 the chemical composition of the leaf-fall and topsoil of the two species (Fig. 4) indicated that
386 nutrient concentration in the topsoil was strongly related to that measured in the leaf-fall, as
387 evidenced by the correlation of all variables along the main axis. This meant that the foliage
388 attributes (in this case chemical composition) of each tree were mirrored in the topsoil, which
389 was consistent with a leaf-fall-mediated tree species effect on soil properties.

390 We conducted a more detailed study on the chemical composition along the soil profile
391 beneath *Q. canariensis* and *Q. suber* in La Saucedá (Fig 5). Samples were taken every 10 cm

392 along the first 0-60 cm of soil. In accordance to the previous results, differences in soil
393 nutrient concentration between species were larger in the uppermost soil layers but they
394 gradually disappeared with soil depth.

395 One of the key issues when examining tree species induced soil changes is the confounding
396 effect of soil variability prior to species establishment. If experiments are conducted on an
397 initially homogeneous substrate, then any changes in soil variables between species can be
398 fully attributed to species effects. Otherwise differences in the soils under different species
399 may not conclusively confirm the species ability to modify soil conditions, but could be the
400 result of the initial species distribution governed by the differences in species soil and
401 nutrient requirements. As a result most studies investigate tree species influence on soil
402 conditions using experimental plantations with monocultures in common garden designs on
403 homogeneous substrates (Menyailo *et al.*, 2002; Hagen-Thorn *et al.*, 2004; Oostra *et al.*, 2006;
404 Vesterdal *et al.*, 2008). Descriptive studies from mixed forests overcome this limitation by
405 assessing the homogeneity of the deeper soil layers, as a surrogate of the initial substrate
406 conditions (Boettcher and Kalisz, 1990; Finzi *et al.*, 1998a; Finzi *et al.*, 1998b). In mature
407 (50-100 years old), stands species influence can be found in the deeper mineral soils layer
408 (Nordén, 1994). However changes in soil chemistry due to differences in leaf-fall quality are
409 much more distinct in the upper most layers, as was the case in the studied forest (Hagen-
410 Thorn *et al.*, 2004).

411 Our study focussed on the effects via leaf-fall properties but other concurrent mechanisms
412 might also induce changes in the soil conditions, such as differences in interception of
413 atmospheric deposition, canopy interactions, leaching and root exudates as well as alterations
414 to microclimate (Augusto *et al.*, 2002; Berger *et al.*, 2009). However, the strong relationship
415 between the chemical composition of the leaf-fall and the soil beneath the canopy of each
416 tree, and the finding that the differences between oak species declined with depth in the soil
417 profile suggest that the changes in soil chemistry were largely due to leaf-fall properties.

418 3.5. *Soil microbial biomass*

419 Soil microbial biomass (C_{mic}) and microbial nutrients (N_{mic}, P_{mic}) were higher under *Q.*
420 *canariensis* than under *Q. suber* (18%; 24%; 9% respectively), as reported by Aponte *et al.*
421 (2010b). To determine whether this effect was mediated by tree species influence on soil
422 properties we analysed the covariation of microbial nutrients and soil properties (Fig 6). Two

423 main significant axes accounting for 34% and 18% of the variance emerged from the
424 ordination analysis as determined by the broken stick method. The variables loading on these
425 two axes revealed that microbial C, N and P variability was strongly related to the abiotic soil
426 properties. The analysis of bivariate relationships indicated that among all soil parameters,
427 soil total N was the best predictor of Cmic ($R^2=0.84$), Nmic ($R^2=0.87$) and Pmic ($R^2=0.69$).

428 Several studies have reported differences in microbial C, N and P in soils from under
429 different tree species (Malchair and Carnol, 2009; Smolander and Kitunen, 2011; Huang *et al.*,
430 *et al.*, 2013). In most cases the mechanisms underlying those effects remain unclear, while
431 others found that microbial biomass was positively related to the availability of limiting
432 resources such as water, organic matter and nutrients (Billore *et al.*, 1995; Nielsen *et al.*,
433 2009; Lucas-Borja *et al.*, 2012). Therefore the increased levels of soil microbial C, N and P
434 under *Q. canariensis* could be explained by the higher nutrient concentrations (particularly
435 total N), soil organic matter content and soil water-holding capacity of its soils as compared
436 to *Q. suber*. Furthermore, Aponte *et al.* (2010b) observed a positive correlation between
437 microbial and available inorganic N and P ($r=0.44$ and $r=0.37$ respectively; $p<0.001$). These
438 relationships suggest that tree species, through their influence on soil microorganisms, can
439 affect nutrient mineralization and availability further reinforcing their effect on soil fertility
440 (Smolander and Kitunen, 2011; Huang *et al.*, 2013).

441 The differences observed by Aponte *et al.* (2010b) in the microbial pools between *Quercus*
442 species were only significant in the uppermost soil layer (0-8 cm) whereas they diluted with
443 soil depth (8-16 cm). The pattern of differences in microbial nutrients (being greatest in the
444 upper soil and disappearing along the soil profile) mirrored that found for soil nutrient
445 concentrations (Fig. 5). Furthermore, these layers (0-8 cm and 8-16 cm) would roughly
446 correspond to the organic F and H layers, as the average depth of the organic soil in these
447 sites was 20 cm. The F layer often shows the largest differences in microbial communities
448 composition and activity among tree species as opposed to the H layer and the mineral soil,
449 which are less influenced by tree species and thus show less detectable differences (Grayston
450 and Prescott, 2005; Ushio *et al.*, 2010). Root litter and root exudates could also influence
451 microbial communities through input of labile C and nutrients (Billore *et al.*, 1995;
452 Brimecombe *et al.*, 2000). However the correlation between soil and microbial nutrients and
453 the dilution of differences between species along the vertical soil profile suggest that species

454 indirectly affected soil microbial biomass through leaf-fall-mediated changes in soil abiotic
455 properties.

456 Both Nmic and Pmic showed a strong seasonal variability, with differences between species
457 being significant in spring but not in summer (Aponte *et al.*, 2010b). This was attributed to
458 changes in soil water content, which varied almost two-fold from spring (21%) to summer
459 (12%). That is, drought limited microbial activity during summer, equalising the levels of
460 Nmic and Pmic between species. However high soil water availability in spring increased the
461 accessibility of nutrients (Nielsen *et al.*, 2009), thus allowing for a differential microbial
462 growth beneath the two *Quercus*. Higher microbial activity in the wet than in the dry season
463 had been previously found in the same forest (Quilchano and Marañón, 2002). The effect of
464 changes in water availability could further interact with seasonal differences in substrate
465 availability associated to species phenology (Rinnan *et al.*, 2008). In the studied forest, the
466 evergreen *Q. suber* showed a clear seasonal pattern, shedding most of its annual leaf-fall
467 during early summer as a strategy to reduce evapo-transpiration and withstand summer
468 drought (Supplementary Figure S1). In contrast the winter deciduous *Q. canariensis* had
469 marcescent habit and shed most (60%) of its leaf-fall throughout the winter and spring
470 (Navarro *et al.*, 2005). Therefore, *Q. canariensis* provided more and higher quality substrate
471 at the peak time of microbial activity, explaining why the differences observed in the soil
472 microbial properties between the two oaks were significant only in spring.

473 3.6. *Ectomycorrhizal community composition*

474 The ECM community on the roots of *Q. canariensis* and *Q. suber* was examined to evaluate
475 to which extent host species and host-generated soil conditions influenced the symbiotic
476 community (Aponte *et al.* 2010a). The ECM community composition of the two oaks was
477 largely dissimilar with only 13 of the 69 identified species (18%) occurring in both *Quercus*
478 species. *Thelephoraceae* species dominated the roots of *Q. canariensis* (38.9% of the
479 identified mycorrhizae) whereas species from *Russulaceae* family dominated the roots of *Q.*
480 *suber* (46.6%). The taxonomic distinctness (Warwick and Clarke, 1995) and the phylogenetic
481 structure of the community also shifted between oak species ($P < 0.001$): *Q. canariensis*
482 harboured a segregated phylogeny (lower taxonomic distinctness) with a high abundance of
483 the resupinate tomentelloid species and a lack of epigeous taxa. In contrast, *Q. suber* ECM
484 community showed a high taxonomic distinctness (i.e., lower phylogenetic relatedness
485 among species) and a higher abundance of epigeous species.

486 The shift in ECM species composition was related to changes in litter and topsoil properties
487 (Aponte *et al.* 2010a). In particular, Ca concentration emerged as the best predictor of the
488 ECM community composition ($P < 0.001$; 8% of the overall ECM species variance). Calcium
489 concentrations were strongly related to soil pH suggesting that calcium-induced changes in
490 soil acidity could also be driving the shift observed in the fungal communities. Based on their
491 observations of distinct Ca contents of the leaf-fall, litter and topsoil of *Q. canariensis* and *Q.*
492 *suber* they conducted a path analysis to evaluate whether the changes in the ECM
493 composition could be attributed to the leaf-fall mediated changes on the litter and topsoil Ca
494 concentrations (Supplementary Figure S3). Several alternative models were tested but only
495 those which included the indirect effects of host species on litter and topsoil properties *via*
496 leaf-fall Ca were significant as opposed to those which only included the direct effects of soil
497 or host species. These results suggested that *Q. canariensis* and *Q. suber* influenced the ECM
498 community composition by altering litter and topsoil acidity and Ca concentration.

499 Other studies have observed shifts in the composition of the ECM fungal communities, such
500 as changes in species richness and dominance from epigeous to resupinate and from
501 Basidiomycetes to Ascomycetes, related to variations in soil nutrient availability (Avis *et al.*,
502 2008; Buée *et al.*, 2011; Kluber *et al.*, 2012). Under high nutrient availability tree dependence
503 on ECM symbiosis for nutrient uptake decreases and so might the transference of
504 carbohydrates to the symbionts. This would favour the presence of tomentelloid species,
505 which have certain saprophytic capacity and are able to obtain part of their carbon through
506 litter and soil organic matter decomposition (Kõljalg *et al.*, 2000; Pena *et al.*, 2013). Thus the
507 soil conditions generated by *Q. canariensis* imposed an environmental filter selecting for a
508 cluster of closely related ‘tolerant’ species. On the other hand, the higher taxonomic
509 distinctness observed in the nutrient-poor soils under *Q. suber* suggests a functional
510 diversification of the ECM community driven by limiting resources and competitive
511 interactions. Soil acidity has also been shown to affect species performances (e.g., production
512 of fruit bodies, mycelial growth, enzymatic capabilities) and thus influence their competitive
513 abilities leading to changes in the community composition (Agerer *et al.*, 1998; Rosling *et al.*,
514 2004 ; Courty *et al.*, 2005). Nonetheless, these changes were treated as abiotic host-
515 independent influence. Morris *et al.* (2008) conducted a similar study to Aponte *et al.* (2010a)
516 and also found differences in the abundance and diversity of epigeous ECM species between
517 the roots of coexisting evergreen and deciduous oaks and related those differences with
518 changes in host species and soil nutrient content. However, in contrast to Aponte *et al.*

519 (2010), they did not attempt to demonstrate the soil-mediated indirect effect of host tree
520 species on ECM fungal assemblages.

521 Tree species effect on ECM fungi could further lead to changes in the microbial community
522 activity and composition as their production of exudates can further affect other soil
523 microorganisms (Högberg and Högberg, 2002; Jones *et al.*, 2004; Frey-Klett *et al.*, 2005).
524 Some studies have related changes in the microbial community composition (PLFA, TRFLP)
525 with variation in litter and soil pH and Ca (Ayres *et al.*, 2009; Thoms *et al.*, 2010). Whether
526 these changes are mediated by shifts in the ECM community composition remains unclear.
527 The recent increase in the number of studies exploring the indirect effects of plant species on
528 soil communities highlights the important role that these interactions have in the ecosystem
529 functioning (Thoms *et al.*, 2010; Sagova-Mareckova *et al.*, 2011; Lucas-Borja *et al.*, 2012;
530 Mitchell *et al.*, 2012; Vesterdal *et al.*, 2012).

531 3.7. Feedback effects and species coexistence

532 The mechanisms sustaining evergreen and deciduous species coexistence are still unclear
533 (Givnish, 2002). Most studies suggest that species coexistence is maintained by differences in
534 their regeneration niche, demographic characteristics, susceptibility to soil pathogens or
535 responses to gap disturbance regime (Tang and Ohsawa, 2002; Taylor *et al.*, 2006; Gómez-
536 Aparicio *et al.*, 2012). In a recent analysis of the mechanisms promoting species coexistence
537 Barot *et al.*(2004) suggested that species-induced spatial heterogeneity of resources
538 ('endogenous heterogeneity') could sustain species coexistence through self-generated niche
539 differentiation. For example, if the species-specific changes in ecosystem properties
540 generated a positive feedback by leading to soil conditions in which the species are more
541 competitive, then the endogenous environmental heterogeneity would promote stable species
542 coexistence through space partitioning (Pacala and Levin, 1997; Brandt *et al.*, 2013). Our
543 results indicated that coexisting deciduous *Q. canariensis* and evergreen *Q. suber*, through
544 their capacity to modify the soil properties and communities beneath their canopies, created a
545 mosaic of soil conditions, i.e. endogenous environmental heterogeneity. However, only if the
546 species' self-generated soil conditions increased their own fitness in a positive feedback
547 would this heterogeneity promote coexistence. Aponte *et al.* (2011) tested the feasibility of
548 this positive feedback effect using a path analysis that fitted several alternative causal models
549 to the empirical data collected on the field. In particular they analysed the causal relationships
550 between the oak species and the chemical composition of the fresh leaves, leaf-fall, topsoil

551 and subsoil (Supplementary Figure S4). The main hypothesis underlying the models tested
552 were (1) oak species affect soil conditions via nutrient return, and in turn this affects species
553 distribution and generates a positive feedback effect; (2) species modify topsoil conditions
554 via nutrient return but species distribution is only affected by subsoil properties, thus there
555 are no feedback effects; and (3) soil affects species distribution, but trees have no effect on
556 soil conditions. Only the model based on the feedback hypothesis matched field data. Also,
557 observational and experimental works in the study area have shown that the studied *Quercus*
558 species differ in their regeneration niches, as mentioned above (section 3.1). The probability
559 of successful recruitment, growth rate and abundance of seedlings and saplings of both oaks
560 was positively related to the presence of conspecific adults and negatively related to the
561 presence of the other species (Maltez-Mouro *et al.*, 2005; Pérez-Ramos *et al.*, 2010). In
562 addition, the emergence and recruitment of *Q. canariensis* increased with soil fertility
563 (Maltez-Mouro *et al.*, 2009; Pérez-Ramos and Marañón, 2012). Furthermore, the soil
564 conditions generated by each species aligns with their life-history and nutritional strategies
565 and reflect, at a local scale, the different environments where each species dominate (Gómez-
566 Aparicio *et al.*, 2008b; Urbietta *et al.*, 2008; Pérez-Ramos *et al.*, 2010). All of the above
567 suggest that each oak species generates a space where it is the best competitor, leading to a
568 potential positive feedback effect that would underpin species coexistence (Catovsky and
569 Bazzaz, 2000; Barot, 2004; Brandt *et al.*, 2013).

570 The importance of the role of plant-soil feedbacks as drivers of plant community composition
571 and species coexistence is increasingly being recognized (Gómez-Aparicio *et al.*, 2008a;
572 Kulmatiski *et al.*, 2008; Kardol *et al.*, 2013). For instance, Brandt *et al.* (2013) observed that
573 soil heterogeneity generated by plant-soil feedbacks had species-specific effects on
574 germination and establishment, with consequences for recruitment dynamics. Interestingly,
575 most reported plant-soil feedback effects are negative, often mediated by soil pathogens and
576 root herbivores (Bever, 2003; Bonanomi *et al.*, 2005; Kardol *et al.*, 2006; Kulmatiski and
577 Kardol, 2008). Gómez-Aparicio *et al.* (2012) analysed the spatial patterns of soil pathogens in
578 *Q. canariensis* – *Q. suber* mixed forests and found no evidence of plant-soil feedback effects
579 *via* soil pathogens. Furthermore, as stated in a recent review on plant-soil feedbacks (van der
580 Putten *et al.*, 2013), most negative feedbacks results emerge from simulations, monoculture
581 experiments under controlled indoor conditions or field studies in agricultural systems.
582 Feedback studies in natural forest systems are still scarce and essential to understand plant
583 population dynamics and functioning of forest ecosystems.

584 Although this empirical evidence sustains our hypothesis regarding the capacity of oak
585 species to modify ecosystem properties, our conclusions on the positive feedback processes
586 and coexistence mechanisms are tentative. Reciprocal field-based transplant experiments
587 where species are planted next to con- and hetero-specific individuals are pathways for future
588 investigations into the tree-soil feedbacks in these mixed oak forest. Glasshouse experimental
589 approaches such addition of soil inocula in sterilized soils and soil conditioning by ‘own’ vs.
590 ‘foreign’ plant species could further help teasing apart the influence of the biotic and abiotic
591 soil conditioning on the feedback processes (Brinkman *et al.*, 2010; Brandt *et al.*, 2013)}.

592 4. CONCLUSIONS

593 We have reviewed the existing knowledge on multiple and concurrent tree-soil interactions in
594 a mixed forest of deciduous *Q. canariensis* and evergreen *Q. suber*. In this forest, oak species
595 leaf-fall quality (particularly nutrient content) determined nutrient return, leaf-fall
596 decomposition and nutrient release into soil, leading to different levels of soil fertility. In turn
597 oak species generated changes in soil nutrient concentrations, particularly N and Ca, further
598 affected the size and composition of the soil microbial community. Through this integration
599 we have gained a comprehensive understanding of the mechanisms underlying oak species
600 effect on soil abiotic properties and soil communities. In addition, we have presented
601 evidence supporting the hypothesis that tree-species-induced changes in soil conditions create
602 a positive feedback which favours tree species coexistence though niche partitioning.
603 Understanding the mechanisms sustaining long-term species coexistence in mixed
604 communities is critical to foresee changes in the structure and composition of plant
605 communities. Our results reinforce the suggestion that plant-soil feedbacks influence species
606 abundance, persistence and succession and thereby underpin species coexistence (Bonanomi
607 *et al.*, 2005; Brandt *et al.*, 2013; van der Putten *et al.*, 2013).

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963 FIGURE LEGENDS

964 Figure 1. a) . PCA ordination of leaf traits of the woody plant species sampled at La Saucedá,
965 including *Q. canariensis* (filled symbol) and *Q. suber* (hollow symbol). Species scores
966 represent the centroid of 5 individuals of the same species except for the *Quercus* (modified
967 from Domínguez *et al.*, (2012)). b) PCA ordination of 20 individuals of *Q. canariensis* and *Q.*
968 *suber* sampled in La Saucedá and Tiradero. Abbreviations are LMA: leaf mass per area,
969 LDMC: leaf dry matter content, d15N: isotope N¹⁵, d13C: isotope C¹³ and symbols of each
970 element indicating their concentration in fresh leaves.

971 Figure 2. Correlation between the chemical composition of the fresh leaves and leaf-fall for
972 the evergreen *Q. suber* and the deciduous *Q. canariensis*. Dots represent the average value of
973 the element concentration for 20 evergreen and 20 deciduous trees.

974 Figure 3. Differences in nutrient loss from litter during decomposition of leaf-fall of the
975 deciduous *Q. canariensis* (filled symbol) and the evergreen *Q. suber* (hollow symbol).

976 Figure 4. PCA ordination of the chemical composition of the leaf-fall (LF) and topsoil (TOP)
977 of 20 *Q. canariensis* (filled symbols) and 20 *Q. suber* (hollow symbols) sampled in La
978 Saucedá and Tiradero. Differences (ANOVA) between *Q. canariensis* and *Q. suber* scores
979 along the factor1 axis are indicated.

980 Figure 5. Variation in N, Ca and P concentrations along the soil vertical profile beneath the
981 canopy of the deciduous *Q. canariensis* (filled symbol) and the perennial *Q. suber* (hollow
982 symbols).

983 Figure 6. PCA ordination of the properties of soil and soil microbial biomass in the upper 0-8
984 cm measured in spring (Sp) and summer (Su) under *Q. canariensis* (filled symbols) and *Q.*
985 *suber* (hollow symbols). Differences (ANOVA) between *Q. canariensis* and *Q. suber* scores
986 along the factor1 axis are indicated.

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Figure 1.

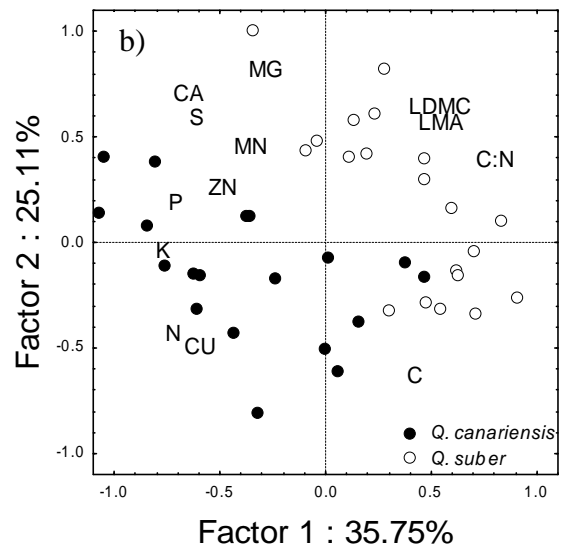
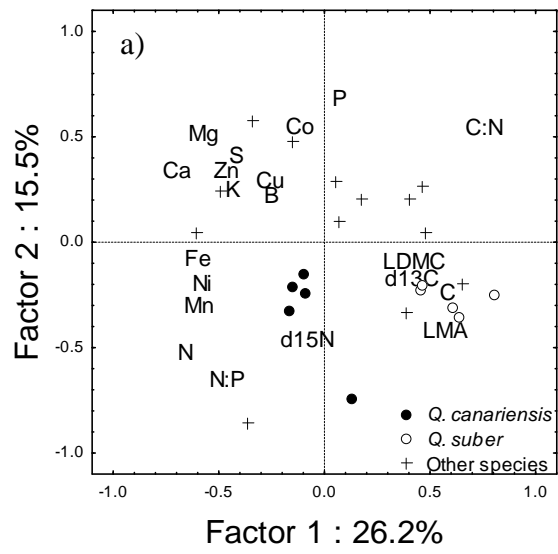


Figure 2.

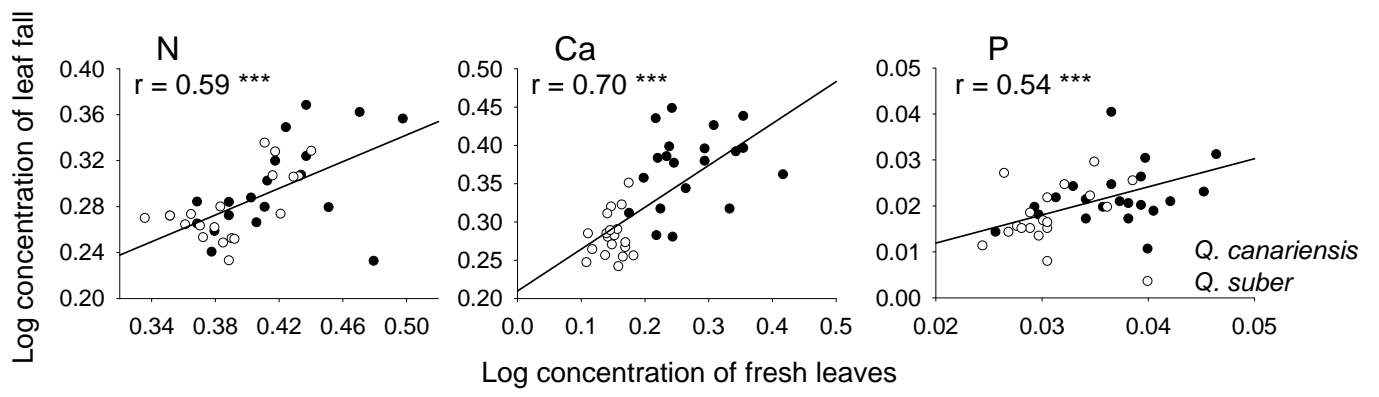


Figure 3.

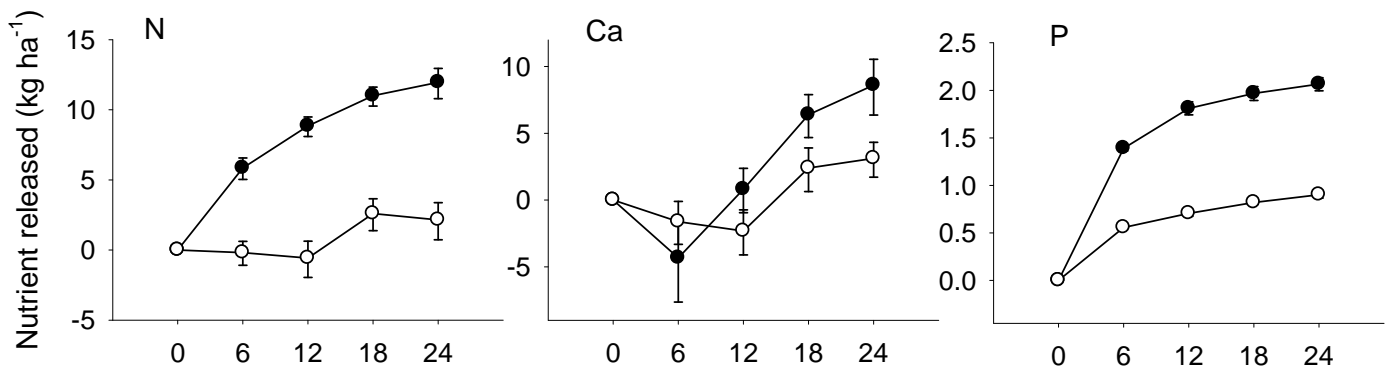


Figure 4.

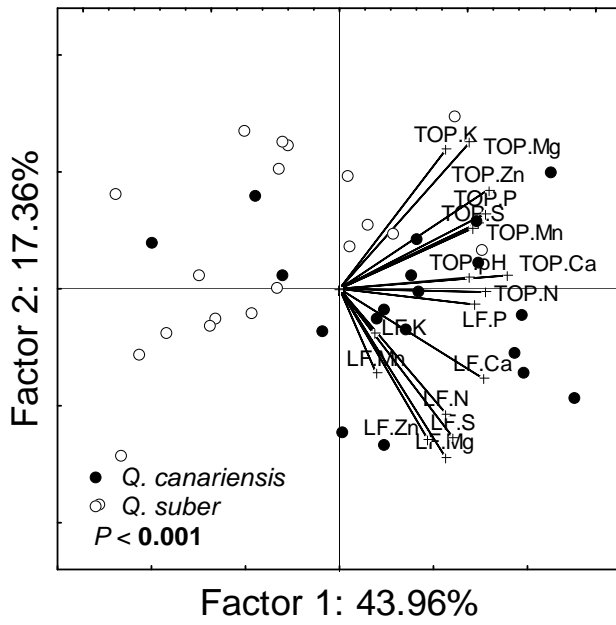


Figure 5.

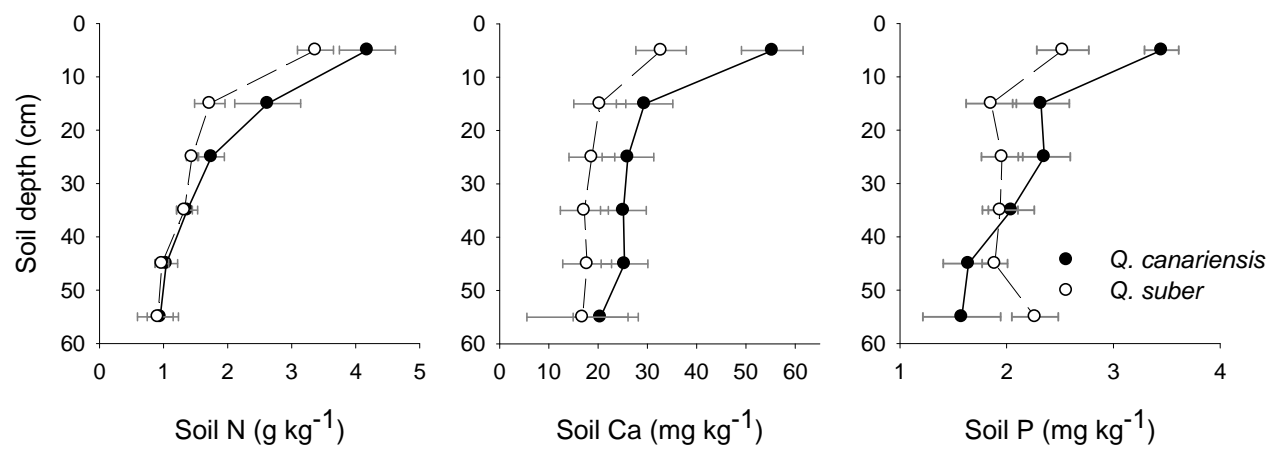
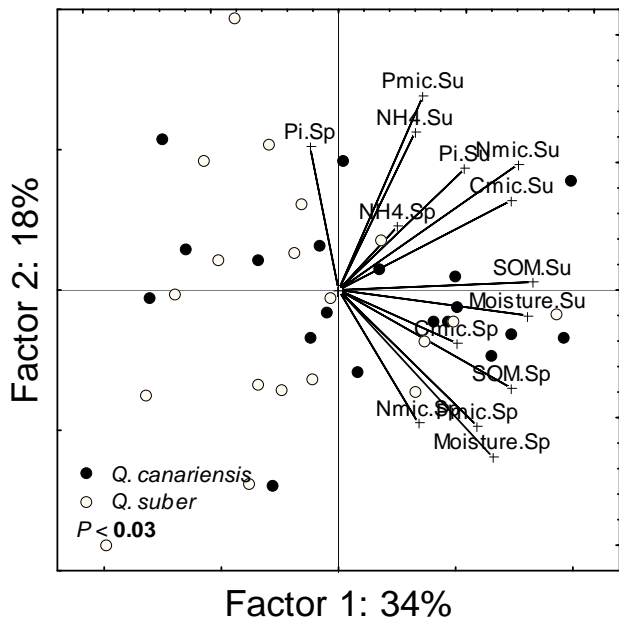


Figure 6.



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Tree species effects on nutrient cycling and soil biota: a feedback mechanism favouring species coexistence.

