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 (Cmic) and nutrients (Nmic, Pmic) 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

1. INTRODUCTION

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

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

Many studies have shown that trees are ecosystem engineers able to generate species-specific effects on soil properties and soil communities that could potentially lead to a feedback effect (Gómez-Aparicio and Canham, 2008; Vesterdal *et al.*, 2008; Mitchell *et al.*, 2012; Vesterdal *et al.*, 2012; Prescott and Grayston, 2013 and references therein). However, few of them have investigated the processes underpinning those effects and their consequences for ecosystem properties (Reich *et al.*, 2005; Mitchell *et al.*, 2007; Ayres *et al.*, 2009). Furthermore, these studies are often focused on a particular aspect of tree-soil interactions. For instance, studies have separately addressed tree species effect on light availability, soil chemical properties, decomposer community or the effects of soils on species distributions (Canham *et al.*, 1994; Van Breemen *et al.*, 1997; Hobbie *et al.*, 2006; Turk *et al.*, 2008). To our knowledge only a few studies have presented a holistic vision of the multiple concomitant tree-soil interaction processes occurring at a single site despite its importance to ecosystem functioning (Ayres *et 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 km^2 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 ℃ 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 (Urbieta *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   Sauceda (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 m^2 m^{-2}) compared to La
126   Sauceda (530-560 m a.s.l; 219 stems ha^{-1}; LAI 1.84 m^2 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 Sauceda (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 Sauceda). 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 Sauceda. 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 (δ^{13}C) and N (δ^{15}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 $HCl + HNO_3$ (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 Sauceda, 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

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

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

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

Annual leaf-fall production of *Q. canariensis* and *Q. suber* was similar in amount (0.30 and 0.29 kg/m^2 respectively). Comparable leaf-fall production values were found for the winter deciduous *Q. pyrenaica* (0.237 kg/m^2) in the centre of Spain (Salamanca), and the evergreens *Q. lanuginose* (0.246 kg/m^2) and *Q. ilex* (0.243 kg/m^2) in the south of France (Montpellier) (Rapp *et al.*, 1999), suggesting that, at least for this genus, leaf-fall productivity is not necessarily related to foliar habit. Both leaf-fall nutrient content and leaf-fall quantity determine tree species nutrient return and their impact on ecosystem properties (Facelli and Pickett, 1991; Washburn and Arthur, 2003). Leaf-fall quantity could be more influential than quality in terms of net nutrient return to soil if the different masses of leaf-fall overrode the differences in nutrient concentrations (Chabot, 1982; Cuevas and Lugo, 1998). However this was not the case for *Q. suber* and *Q. canariensis*, which had comparable leaf-fall production. Therefore the nutrient concentration of the leaf-fall created the distinct nutrient return of the two species.

3.3. *Leaf-fall decomposition and nutrient release*

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

In contrast to the pattern observed during early decomposition, the limit value of decomposition, i.e. the fraction of leaf litter mass that remains stable at late stages of decomposition and builds up soil organic matter, was higher for *Q. canariensis* than for *Q. suber* (40% *vs.* 31%, p<0.0001; Aponte *et al.* 2012). This was consistent with the larger concentrations of soil organic matter measured under the canopy of *Q. canariensis* than under *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 subtrate (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 Sauceda (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 subtrates (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 (Cmic) and microbial nutrients (Nmic, Pmic) 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

15

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

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

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

17

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

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

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

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

6. REFERENCES

Aerts, R., 1995. The advantages of being evergreen. Trends Ecol Evol 10, 402-407.

Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? J Ecol, 597-608.

Aerts, R., De Caluwe, H., Beltman, B., 2003. plant community mediated vs. nutritional controls on litter decomposition rates in grasslands. Ecology 84, 3198-3208.

Agerer, R., Taylor, A.F.S., Treu, R., 1998. Effects of acid irrigation and liming on the production of fruit bodies by ectomycorrhizal fungi. Plant and Soil 199, 83-89.

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Caceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J., Strauss, S., Turner, M.G., Werner, E., 2007. Filling key gaps in population and community ecology. 5, 145-152.

Anonymous, 2005. PORN / PRUG / PDS Parque Natural Los Alcornocales. Junta de Andalucía, Consejería de Medio Ambiente, Sevilla, España.

Aponte, C., García, L.V., Marañón, T., Gardes, M., 2010a. Indirect host effect on ectomycorrhizal fungi: Leaf fall and litter quality explain changes in fungal communities on the roots of co-occurring Mediterranean oaks. Soil Biol. Biochem. 42, 788-796.

Aponte, C., García, L.V., Pérez-Ramos, I.M., Gutiérrez, E., Marañón, T., 2011. Oak trees and soil interactions in Mediterranean forests: a positive feedback model. J. Veg. Sci. 22, 856-867.

Aponte, C., Garcia V., L., Marañón, T., 2012. Tree species effect on litter decomposition and nutrient release in Mediterranean oak forests change over time. Ecosystems 15, 1204-1218.

Aponte, C., Marañón, T., García, L.V., 2010b. Microbial C, N and P in soils of Mediterranean oak forests: influence of season, canopy cover and soil depth. Biogeochemistry 101, 77-92.

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59, 233-253.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442, 555-558.

Avis, P.G., Mueller, G.M., Lussenhop, J., 2008. Ectomycorrhizal fungal communities in two North American oak forests respond to nitrogen addition. New Phytol. 179, 472-483.

Ayres, E., Steltzer, H., Berg, S., Wallenstein, M.D., Simmons, B.L., Wall, D.H., 2009. Tree Species Traits Influence Soil Physical, Chemical, and Biological Properties in High Elevation Forests. PLoS ONE 4, e5964.

Barot, S., 2004. Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? Oikos 106, 185-192.

Berg, B., De Santo, A.V., Rutigliano, F.A., Fierro, A., Ekbohm, G., 2003. Limit values for plant litter decomposing in two contrasting soils: influence of litter elemental composition. Acta Oecologica 24, 295-302.

Berger, T.W., Untersteiner, H., Toplitzer, M., Neubauer, C., 2009. Nutrient fluxes in pure and mixed stands of spruce (Picea abies) and beech (Fagus sylvatica). Plant and Soil 322, 317-342.

661   Bever, J.D., 1994. Feeback between Plants and Their Soil Communities in an Old Field Community.
662   Ecology 75, 1965-1977.
663   Bever, J.D., 2003. Soil community feedback and the coexistence of competitors: conceptual
664   frameworks and empirical tests. New Phytol. 157, 465-473.
665   Billore, S.K., Ohsawa, M., Numata, M., Okano, S., 1995. Microbial biomass nitrogen pool in soils
666   from a warm temperate grassland, and from deciduous and evergreen forests in Chiba, central
667   Japan. Biology and Fertility of Soils 19, 124-128.
668   Blaxter, M., Mann, J., Chapman, T., Thomas, F., Whitton, C., Floyd, R., Abebe, E., 2005. Defining
669   operational taxonomic units using DNA barcode data. Philosophical Transactions of the Royal
670   Society B: Biological Sciences 360, 1935-1943.
671   Boettcher, S.E., Kalisz, P.J., 1990. Single-tree influence on soil properties in the mountains of eastern
672   Kentucky. Ecology 71, 1365-1372.
673   Bonanomi, G., Giannino, F., Mazzoleni, S., 2005. Negative plant–soil feedback and species
674   coexistence. Oikos 111, 311-321.
675   Brandt, A.J., de Kroon, H., Reynolds, H.L., Burns, J.H., 2013. Soil heterogeneity generated by plant–
676   soil feedbacks has implications for species recruitment and coexistence. J Ecol 101, 277-286.
677   Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic and available forms of phosphorous in
678   soils. Soil Science 59, 39-45.
679   Brimecombe, M.J., De Leij, F.A., Lynch, J.M., 2000. The effect of root exudates on rhizosphere
680   microbial populations. Biochemistry and Organic Substances at the Soil-Plant Interface. The
681   Rhizosphere, Biochemistry and Organic Substances at the Soil-Plant Interface. Marcel Dekker,
682   New York, 95-140.
683   Brinkman, E.P., Van der Putten, W.H., Bakker, E.-J., Verhoeven, K.J.F., 2010. Plant–soil feedback:
684   experimental approaches, statistical analyses and ecological interpretations. J Ecol 98, 1063-1073.
685   Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the
686   release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in
687   soil. Soil Biol. Biochem. 17, 837-842.
688   Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurment of microbial phosphorus in soil.
689   Soil Biol. Biochem. 14, 319-329.
690   Buée, M., Maurice, J.-P., Zeller, B., Andrianarisoa, S., Ranger, J., Courtecuisse, R., Marçais, B., Le
691   Tacon, F., 2011. Influence of tree species on richness and diversity of epigeous fungal
692   communities in a French temperate forest stand. Fungal Ecology 4, 22-31.
693   Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource
694   heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian
695   Journal of Forest Research 24, 337-349.
696   Catovsky, S., Bazzaz, F.A., 2000. The role of resource interactions and seedling regeneration in
697   maintaining a positive feedback in hemlock stands. J Ecol 88, 100-112.
698   Chabot, B.F., 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics 13,
699   229.
700   Chadwick, D.R., Ineson, P., Woods, C., Piearce, T.G., 1998. Decomposition of *Pinus sylvestris* litter
701   in litter bags: Influence of underlying native litter layer. Soil Biol. Biochem. 30, 47-55.
702   Cornelissen, J., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D., Reich, P., ter Steege,
703   H., Morgan, H., van der Heijden, M., Pausas, J., Poorter, H., 2003. A handbook of protocols for
704   standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335-380.
705   Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-
706   Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic
707   matter stabilization: do labile plant inputs form stable soil organic matter? Glob Change Biol 19,
708   988-995.
709   Courty, P.-E., Pritsch, K., Schloter, M., Hartmann, A., Garbaye, J., 2005. Activity profiling of
710   ectomycorrhiza communities in two forest soils using multiple enzymatic tests. New Phytol. 167,
711   309-319.
712   Cuevas, E., Lugo, A.E., 1998. Dynamics of organic matter and nutrient return from litterfall in stands
713   of ten tropical tree plantation species. For. Ecol. Manage. 112, 263-279.
714   Davey, M.P., Berg, B., Emmett, B.A., Rowland, P., 2007. Decomposition of oak leaf litter is related
715   to initial litter Mn concentrations. Can. J. Bot.-Rev. Can. Bot 85, 16-24.

Diaz, S., Hodgson, J., Thompson, K., Cabido, M., Cornelissen, J., Jalili, A., Montserrat-Martí, G., Grime, J., Zarrinkamar, F., Asri, Y., Band, S., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M., Shirvany, F., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M., 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veg. Sci. 15, 295-304.

Domínguez, M.T., Aponte, C., Pérez-Ramos, I.M., García, L.V., Villar, R., Marañón, T., 2012. Relationships between leaf morphological traits, nutrient concentrations and isotopic signatures for Mediterranean woody plant species and communities. Plant and Soil 357, 407-424.

Ehrenfeld, J.G., Ravit, B., Elgersma, K., 2005. Feedback in the plant-soil system. Annual Review of Environment and Resources 30, 75-115.

Eriksson, K.-E., Blanchette, R.A., Ander, P., 1990. Microbial and enzymatic degradation of wood and wood components. Springer, Verlag, Berlin.

Facelli, J.M., Pickett, S., 1991. Plant litter: Its dynamics and effects on plant community structure. Bot. Rev. 57, 1-32.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40, 503-537.

Finzi, A.C., Canham, C.D., Van Breemen, N., 1998a. Canopy tree-soil interactions within temperate forests: Species effects on pH and cations. Ecol Appl 8, 447-454.

Finzi, A.C., Van Breemen, N., Canham, C.D., 1998b. Canopy tree-soil interactions within temperate forests: Species effects on soil carbon and nitrogen. Ecol Appl 8, 440-446.

Freschet, G.T., Aerts, R., Cornelissen, J.H.C., 2012. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. J Ecol 100, 619-630.

Frey-Klett, P., Chavatte, M., Clausse, M.-L., Courrier, S., Roux, C.L., Raaijmakers, J., Martinotti, M.G., Pierrat, J.-C., Garbaye, J., 2005. Ectomycorrhizal symbiosis affects functional diversity of rhizosphere fluorescent pseudomonads. New Phytol. 165, 317-328.

Gallardo, A., Merino, J., 1993. Leaf decomposition in two Mediterranean ecosystems of southwest Spain: Influence of substrate quality. Ecology 74, 152-161.

García, L.V., Maltez-Mouro, S., Pérez-Ramos, I.M., Freitas, H., Marañón, T., 2006. Counteracting gradients of light and soil nutrients in the undestorey of Mediterranean oak forest. Web Ecology 6, 67-74.

Gardes, M., Bruns, T.D., 1993. ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Molecular Ecology 2, 113-118.

Givnish, T.J., 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. Silva Fennica 36, 703-743.

Gómez-Aparicio, L., Canham, C.D., 2008. Neighborhood models of the effects of invasive tree species on ecosystem processes. Ecol Monogr 78, 69-86.

Gómez-Aparicio, L., Canham, C.D., Martin, P.H., 2008a. Neighbourhood models of the effects of the invasive Acer platanoides on tree seedling dynamics: linking impacts on communities and ecosystems. J Ecol 96, 78-90.

Gómez-Aparicio, L., Ibáñez, B., Serrano, M.S., De Vita, P., Ávila, J.M., Pérez-Ramos, I.M., García, L.V., Esperanza Sánchez, M., Marañón, T., 2012. Spatial patterns of soil pathogens in declining Mediterranean forests: implications for tree species regeneration. New Phytol. 194, 1014-1024.

Gómez-Aparicio, L., Pérez-Ramos, I.M., Mendoza, I., Matías, L., Quero, J.L., Castro, J., Zamora, R., Marañón, T., 2008b. Oak seedling survival and growth along resource gradients in Mediterranean forests: implications for regeneration in current and future environmental scenarios. Oikos 117, 1683-1699.

Grayston, S.J., Prescott, C.E., 2005. Microbial communities in forest floors under four tree species in coastal British Columbia. Soil Biol. Biochem. 37, 1157-1167.

Grime, J.P., 1979. Plant strategies and vegetation processes. Wiley, Chichester.

Hagen-Thorn, A., Callesen, I., Armolaitis, K., Nihlgård, B., 2004. The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land. For. Ecol. Manage. 195, 373-384.

771   Hättenschwiler, S., Jørgensen, H.B., 2010. Carbon quality rather than stoichiometry controls litter
772   decomposition in a tropical rain forest. J Ecol 98, 754-763.
773   Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan
774   tundra. Ecol Monogr 66, 503-522.
775   Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P., 2006.
776   Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87,
777   2288-2297.
778   Högberg, M.N., Högberg, P., 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of
779   microbial biomass and produces, together with associated roots, half the dissolved organic carbon
780   in a forest soil. New Phytol. 154, 791-795.
781   Huang, Z., Wan, X., He, Z., Yu, Z., Wang, M., Hu, Z., Yang, Y., 2013. Soil microbial biomass,
782   community composition and soil nitrogen cycling in relation to tree species in subtropical China.
783   Soil Biol. Biochem. 62, 68-75.
784   Ibrahima, A., Joffre, R., Gillon, D., 1995. Changes in litter during the initial leaching phase: An
785   experiment on the leaf litter of Mediterranean species. Soil Biol. Biochem. 27, 931-939.
786   Jonasson, S., Michelsen, A., Schmidt, I.K., Nielsen, E.V., Callaghan, T.V., 1996. Microbial biomass
787   C, N and P in two arctic soils and responses to addition of NPK fertilizer and sugar: Implications
788   for plant nutrient uptake. Oecologia 106, 507-515.
789   Jones, D.L., Hodge, A., Kuzyakov, Y., 2004. Plant and mycorrhizal regulation of rhizodeposition.
790   New Phytol. 163, 459-480.
791   Jones, J.B., Case, V.W., 1990. Sampling, handling and analyzing plant tissues samples. In:
792   Westerman, R. (Ed.), Soil testing and plant analysis. Soil Science Society of America, Madison,
793   pp. 389-427.
794   Kardol, P., Bezemer, T.M., Putten, W.H.v.d., 2006. Temporal variation in plant-soil feedback controls
795   succession. Ecol Lett 9, 1080-1088.
796   Kardol, P., De Deyn, G.B., Laliberté, E., Mariotte, P., Hawkes, C.V., 2013. Biotic plant–soil
797   feedbacks across temporal scales. J Ecol 101, 309-315.
798   Kluber, L.A., Carrino-Kyker, S.R., Coyle, K.P., DeForest, J.L., Hewins, C.R., Shaw, A.N., Smemo,
799   K.A., Burke, D.J., 2012. Mycorrhizal Response to Experimental pH and P Manipulation in Acidic
800   Hardwood Forests. PLoS ONE 7, e48946.
801   Kõljalg, U., Dahlberg, A., Taylor, A.F.S., Larsson, E., Hallenberg, N., Stenlid, J., Larsson, K.H.,
802   Fransson, P.M., Kårén, O., Jonsson, L., 2000. Diversity and abundance of resupinate thelephoroid
803   fungi as ectomycorrhizal symbionts in Swedish boreal forests. Molecular Ecology 9, 1985-1996.
804   Kulmatiski, A., Beard, K.H., Stevens, J.R., Cobbold, S.M., 2008. Plant-soil feedbacks: a meta-
805   analytical review. Ecol Lett 11, 980-992.
806   Kulmatiski, A., Kardol, P., 2008. Getting Plant—Soil Feedbacks out of the Greenhouse: Experimental
807   and Conceptual Approaches. In: Lüttge, U., Beyschlag, W., Murata, J. (Eds.), Progress in Botany.
808   Springer Berlin Heidelberg, pp. 449-472.
809   Lucas-Borja, M.E., Candel, D., Jindo, K., Moreno, J.L., Andrés, M., Bastida, F., 2012. Soil microbial
810   community structure and activity in monospecific and mixed forest stands, under Mediterranean
811   humid conditions. Plant and Soil 354, 359-370.
812   Malchair, S., Carnol, M., 2009. Microbial biomass and C and N transformations in forest floors under
813   European beech, sessile oak, Norway spruce and Douglas-fir at four temperate forest sites. Soil
814   Biol. Biochem. 41, 831-839.
815   Maltez-Mouro, S., García, L., Freitas, H., 2009. Influence of forest structure and environmental
816   variables on recruit survival and performance of two Mediterranean tree species (*Quercus faginea*
817   *L.* and *Q. suber Lam.)*. European Journal of Forest Research 128, 27-36.
818   Maltez-Mouro, S., García, L., Marañón, T., Freitas, H., 2005. The combined role of topography and
819   overstorey tree composition in promoting edaphic and floristic variation in a Mediterranean forest.
820   Ecological Research 20, 668-677.
821   Marañón, T., Ojeda, J.F., 1998. Ecology and history of a wooded landscape in southern Spain. In:
822   Kirby, K.J., Watkins, C. (Eds.), Ecological History of European Forests. C a B International,
823   Wallingford, pp. 107-116.
824   Menyailo, O., Hungate, B., Zech, W., 2002. Tree species mediated soil chemical changes in a Siberian
825   artificial afforestation experiment. Plant and Soil 242, 171-182.

826 Miki, T., Ushio, M., Fukui, S., Kondoh, M., 2010. Functional diversity of microbial decomposers
827   facilitates plant coexistence in a plant–microbe–soil feedback model. Proceedings of the National
828   Academy of Sciences 107, 14251-14256.
829 Mitchell, R., Keith, A., Potts, J., Ross, J., Reid, E., Dawson, L., 2012. Overstory and understory
830   vegetation interact to alter soil community composition and activity. Plant and Soil 352, 65-84.
831 Mitchell, R.J., Campbell, C.D., Chapman, S.J., Osler, G.H.R., Vanbergen, A.J., Ross, L.C., Cameron,
832   C.M., Cole, L., 2007. The cascading effects of birch on heather moorland: a test for the top-down
833   control of an ecosystem engineer. J Ecol 93, 540-554.
834 Morris, M.H., Smith, M.E., Rizzo, D.M., Rejmanek, M., Bledsoe, C.S., 2008. Contrasting
835   ectomycorrhizal fungal communities on the roots of co-occurring oaks (*Quercus spp.*) in a
836   California woodland. New Phytol. 178, 167-176.
837 Navarro, C.M., Pérez-Ramos, I.M., Marañón, T., 2005. Aporte de hojarasca al suelo en un bosque
838   mediterráneo. Almoraima: Revista de estudios campo gibraltareños 31, 119-127.
839 Negrete-Yankelevich, S., Fragoso, C., Newton, A., Russell, G., Heal, O., 2008. Species-specific
840   characteristics of trees can determine the litter macroinvertebrate community and decomposition
841   process below their canopies. Plant and Soil 307, 83-97.
842 Nielsen, P.L., Andresen, L.C., Michelsen, A., Schmidt, I.K., Kongstad, J., 2009. Seasonal variations
843   and effects of nutrient applications on N and P and microbial biomass under two temperate
844   heathland plants. Applied Soil Ecology 42, 279-287.
845 Nordén, U., 1994. Influence of tree species on acidification and mineral pools in deciduous forest
846   soils of South Sweden. Water Air Soil Pollut 76, 363-381.
847 Norris, M., Avis, P., Reich, P., Hobbie, S., 2012. Positive feedbacks between decomposition and soil
848   nitrogen availability along fertility gradients. Plant and Soil, 1-15.
849 Oostra, S., Majdi, H., Olsson, M., 2006. Impact of tree species on soil carbon stocks and soil acidity
850   in southern Sweden. Scand J Forest Res 21, 364-371.
851 Pacala, S.W., Levin, S.A., 1997. Biologically generated spatial pattern and the coexistence of
852   competing
853 species. In: Tilman, D., Kareiva, P. (Eds.), Spatial Ecology: The Role of Space in Population
854   Dynamics and Interspecific Interactions. Princeton University Press, Princeton, NJ, pp. 204-232.
855 Pena, R., Tejedor, J., Zeller, B., Dannenmann, M., Polle, A., 2013. Interspecific temporal and spatial
856   differences in the acquisition of litter-derived nitrogen by ectomycorrhizal fungal assemblages.
857   New Phytol., doi:10.1111/nph.12272
858 Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J., Vendramini, F., Cabido, M., Castellanos, A., 2000.
859   Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional
860   types and taxa in central Argentina. Plant and Soil 218, 21-30.
861 Pérez-Ramos, I.M., 2007. Factores que condicionan la regeneración natural de especies leñosas en un
862   bosque mediterráneo del sur de la Península Ibérica. In. Universidad de Sevilla, Sevilla.
863 Pérez-Ramos, I.M., Gómez-Aparicio, L., Villar, R., García, L.V., Marañón, T., 2010. Seedling growth
864   and morphology of three oak species along field resource gradients and seed mass variation: a
865   seedling age-dependent response. J. Veg. Sci. 21, 419-437.
866 Pérez-Ramos, I.M., Marañón, T., 2012. Community-level seedling dynamics in Mediterranean
867   forests: uncoupling between the canopy and the seedling layers. J. Veg. Sci. 23, 526-540.
868 Pérez-Ramos, I.M., Roumet, C., Cruz, P., Blanchard, A., Autran, P., Garnier, E., 2012. Evidence for a
869   'plant community economics spectrum' driven by nutrient and water limitations in a
870   Mediterranean rangeland of southern France. J Ecol, n/a-n/a.
871 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of
872   variation in leaf mass per area (LMA): a meta-analysis. New Phytol. 182, 565-588.
873 Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. Tree Physiology 22,
874   1193-1200.
875 Prescott, C.E., Grayston, S.J., 2013. Tree species influence on microbial communities in litter and
876   soil: Current knowledge and research needs. For. Ecol. Manage.
877 Quero, J.L., Villar, R., Marañón, T., Zamora, R., 2006. Interactions of drought and shade effects on
878   seedlings of four Quercus species: physiological and structural leaf responses. New Phytol. 170,
879   819-834.

880 Quilchano, C., Marañón, T., 2002. Dehydrogenase activity in Mediterranean forest soils. Biology and
881   Fertility of Soils 35, 102.
882 Rapp, M., Santa Regina, I., Rico, M., Gallego, H.A., 1999. Biomass, nutrient content, litterfall and
883   nutrient return to the soil in Mediterranean oak forests. For. Ecol. Manage. 119, 39-49.
884 Reich, P., Wright, I., Cavender-Bares, J., Craine, J., Oleksyn, J., Westoby, M., Walters, M., 2003. The
885   evolution of plant functional variation: traits, spectra, and strategies. International Journal of Plant
886   Sciences 164, S143-S164.
887 Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J.,
888   Chadwick, O.A., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil
889   properties: a common garden test with 14 tree species. Ecol Lett 8, 811-818.
890 Rinnan, R., Michelsen, A., Jonasson, S., 2008. Effects of litter addition and warming on soil carbon,
891   nutrient pools and microbial communities in a subarctic heath ecosystem. Applied Soil Ecology
892   39, 271-281.
893 Rosling, A., Lindahl, B.D., Taylor, A.F.S., Finlay, R.D., 2004. Mycelial growth and substrate
894   acidification of ectomycorrhizal fungi in response to different minerals. FEMS Microbiology
895   Ecology 47, 31-37.
896 Sagova-Mareckova, M., Omelka, M., Cermak, L., Kamenik, Z., Olsovska, J., Hackl, E., Kopecky, J.,
897   Hadacek, F., 2011. Microbial communities show parallels at sites with distinct litter and soil
898   characteristics. Applied and Environmental Microbiology 77, 7560-7567.
899 Shipley, B., 2000. Cause and correlation in biology : a user's guide to path analysis, structural
900   equations and causal inference Cambridge University Press, Cambridge, UK.
901 Smolander, A., Kitunen, V., 2011. Comparison of tree species effects on microbial C and N
902   transformations and dissolved organic matter properties in the organic layer of boreal forests.
903   Applied Soil Ecology 49, 224-233.
904 Tang, C.Q., Ohsawa, M., 2002. Coexistence mechanisms of evergreen, deciduous and coniferous trees
905   in a mid-montane mixed forest on Mt. Emei, Sichuan, China. Plant Ecology 161, 215-230.
906 Taylor, A.H., Shi Wei, J., Lian Jun, Z., Chun Ping, L., Chang Jin, M., Jinyan, H., 2006. Regeneration
907   patterns and tree species coexistence in old-growth Abies–Picea forests in southwestern China.
908   For. Ecol. Manage. 223, 303-317.
909 Thoms, C., Gattinger, A., Jacob, M., Thomas, F.M., Gleixner, G., 2010. Direct and indirect effects of
910   tree diversity drive soil microbial diversity in temperate deciduous forest. Soil Biol. Biochem. 42,
911   1558-1565.
912 Tilman, D., 1988. Plant strategies and the dynamics and structure of plant communities. Princeton
913   University Press, Princeton.
914 Turk, T.D., Schmidt, M.G., Roberts, N.J., 2008. The influence of bigleaf maple on forest floor and
915   mineral soil properties in a coniferous forest in coastal British Columbia. For. Ecol. Manage. 255,
916   1874-1882.
917 Urbieta, I.R., Zavala, M.A., Maranón, T., 2008. Human and non-human determinants of forest
918   composition in southern Spain: evidence of shifts towards cork oak dominance as a result of
919   management over the past century. Journal of Biogeography 35, 1688-1700.
920 Ushio, M., Kitayama, K., Balser, T.C., 2010. Tree species-mediated spatial patchiness of the
921   composition of microbial community and physicochemical properties in the topsoils of a tropical
922   montane forest. Soil Biol. Biochem. 42, 1588-1595.
923 Van Breemen, N., Finzi, A.C., Canham, C.D., 1997. Canopy tree - Soil interactions within temperate
924   forests: Effects of soil elemental composition and texture on species distributions. Canadian
925   Journal of Forest Research 27, 1110-1116.
926 van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol,
927   P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Van de Voorde, T.F.J.,
928   Wardle, D.A., 2013. Plant–soil feedbacks: the past, the present and future challenges. J Ecol 101,
929   265-276.
930 Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil
931   microbial biomass C. Soil Biol. Biochem. 19, 703-707.
932 Vesterdal, L., Elberling, B., Christiansen, J.R., Callesen, I., Schmidt, I.K., 2012. Soil respiration and
933   rates of soil carbon turnover differ among six common European tree species. For. Ecol. Manage.
934   264, 185-196.

935 Vesterdal, L., Schmidt, I.K., Callesen, I., Nilsson, L.O., Gundersen, P., 2008. Carbon and nitrogen in
936   forest floor and mineral soil under six common European tree species. For. Ecol. Manage. 255, 35-
937   48.
938 Villar, R., Ruiz-Robleto, J., Jong, Y., Poorter, H., 2006. Differences in construction costs and
939   chemical composition between deciduous and evergreen woody species are small as compared to
940   differences among families. Plant, Cell and Environment 29, 1629-1643.
941 Vivanco, L., Austin, A.T., 2008. Tree species identity alters forest litter decomposition through long-
942   term plant and soil interactions in Patagonia, Argentina. J Ecol 96, 727-736.
943 Warwick, R.M., Clarke, K.R., 1995. New biodiversity measures reveal a decrease in taxonomic
944   distinctness with increasing stress. Marine Ecology Progress Series 129, 301-305.
945 Washburn, C.S.M., Arthur, M.A., 2003. Spatial variability in soil nutrient availability in an oak-pine
946   forest: potential effects of tree species. Can. J. For. Res.-Rev. Can. Rech. For. 33, 2321-2330.
947 White, T.J., Bruns, T., Lee, S., Taylor, J.W., 1990. Amplification and direct sequencing of fungal
948   ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., A, T.J.W.
949   (Eds.), PCR Protocols: A Guide to Methods and Applications. Academic Press, New York, pp.
950   315-322.
951 Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Byron, B.L.,
952   Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I., Westoby, M., 2005.
953   Assessing the Generality of Global Leaf Trait Relationships. New Phytol. 166, 485-496.
954 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J.,
955   Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J.,
956   Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets,
957   U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas,
958   S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum.
959   Nature 428, 821-827.
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963   FIGURE LEGENDS

964   Figure 1. a) . PCA ordination of leaf traits of the woody plant species sampled at La Sauceda,

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 Sauceda and Tiradero. Abbreviations are LMA: leaf mass per area,

969   LDMC: leaf dry matter content, d15N: isotope N^{15}, d13C: isotope C^{13} 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   Sauceda 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
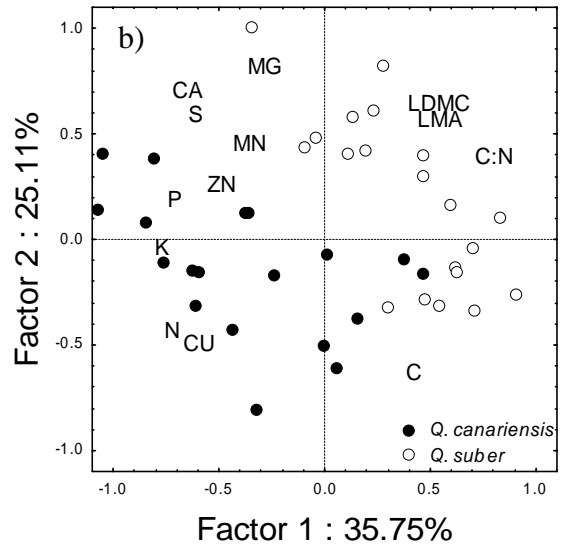
986   along the factor1 axis are indicated.
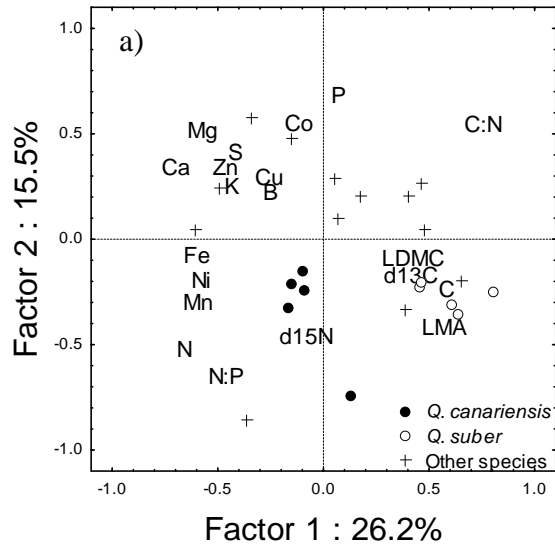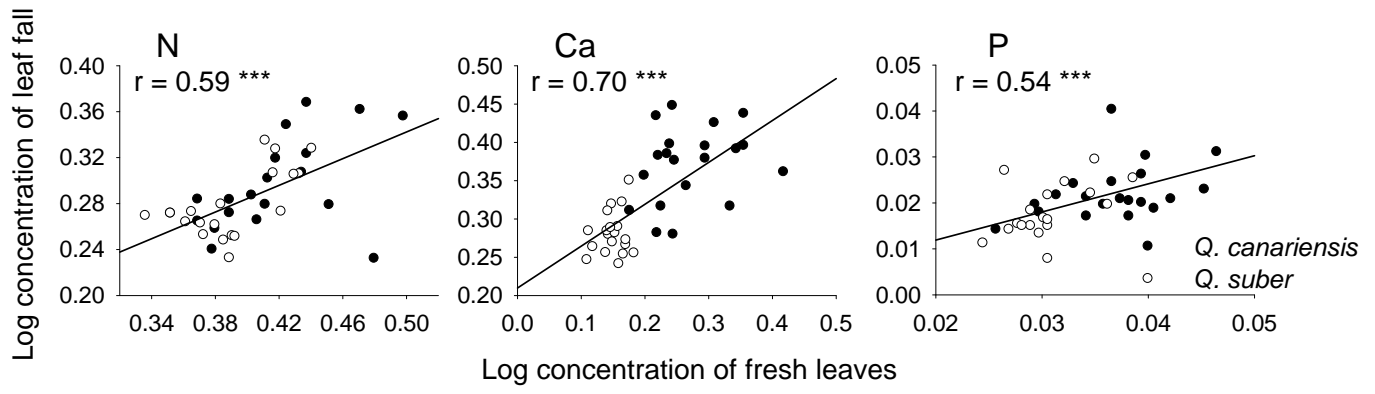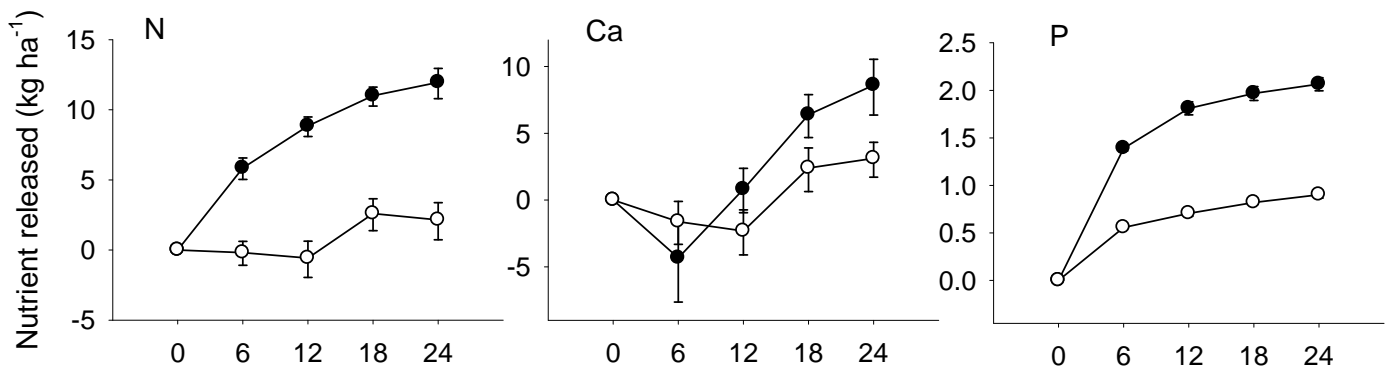
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Figure 1.

Figure 2.

Figure 2.

Figure 3.

Figure 4.

TOP.K TOP.Mg
TOP.Zn
TOP.P
TOP.S
TOP.Mn
TOP.pH TOP.Ca
TOP.N
LF.P
LF.K
LF.Mn
LF.Ca
LF.N
LF.S
LF.Zn LF.Mg

● *Q. canariensis*
○ *Q. suber*
P < **0.001**

Factor 2: 17.36%

Factor 1: 43.96%
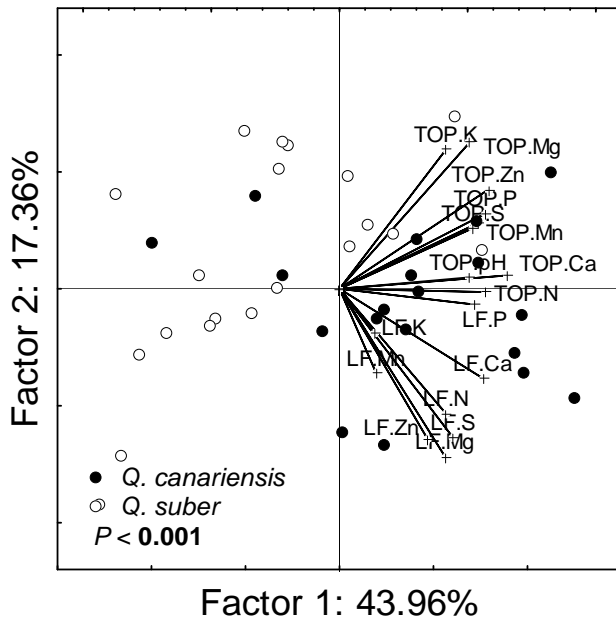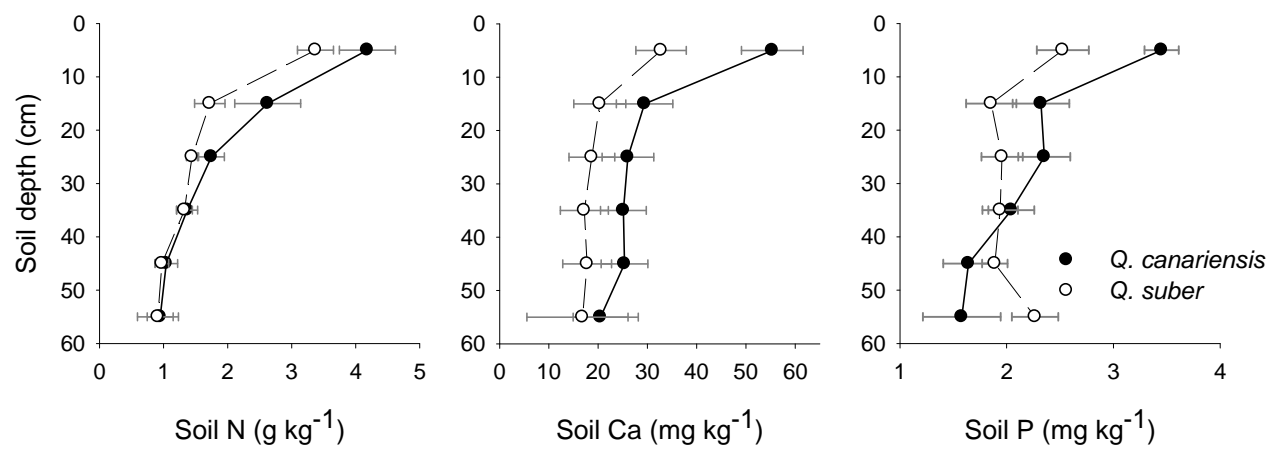
Figure 5.

Figure 6.
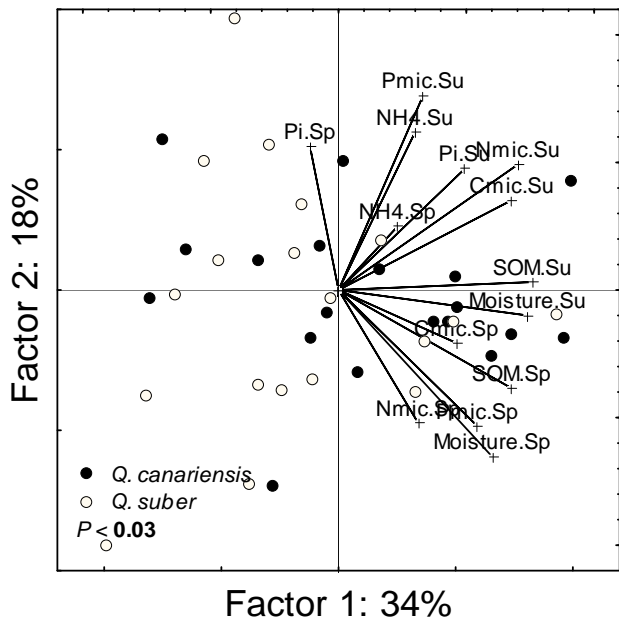
Supplementary Material for online publication only

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

Low chemical quality fresh leaves

Low chemical quality leaf fall

Low nutrient return
Slow decomposition

Nutrient input

Soil nutrient content

Microbial biomass

Evergreen
Q. suber

Deciduous
Q. canariensis

+ Fitness

+ Fitness

High chemical quality fresh leaves

High chemical quality leaf fall

High nutrient return
Fast decomposition

Nutrient input

Soil nutrient content

Microbial biomass

*Reply to reviewers