

Plant Ecology

Populations of *Vaccinium myrtillus* show similar structure and functioning under different scenarios of coexistence at the Pyrenean treeline.

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Abstract:	<p>Plant-plant interactions are key drivers on modulating treeline dynamics. At the Pyrenean treeline, the dwarf shrub <i>Vaccinium myrtillus</i> grows in pure populations or in mixed populations with <i>Vaccinium uliginosum</i> or <i>Rhododendron ferrugineum</i>. They form sparse shrub patches that colonize subalpine grasslands, having dramatic impacts on the structure and functioning of these grassland communities. We investigated the role of the two co-occurring shrubs as possible modulators of <i>V. myrtillus</i> population structure and performance in the Central Pyrenees. We analysed age distribution, growth and functional parameters and N and C cycling (i.e. N and C concentrations and isotope compositions, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of <i>V. myrtillus</i> ramets under these three situations of coexistence. Ramet above-ground biomass and population age structure did not differ between the three situations, but <i>V. myrtillus</i> growing with <i>R. ferrugineum</i> reached greater volumes, a possible response of</p>												

	<p>competition for light. $\delta^{15}\text{N}$ values of <i>V. myrtillus</i> leaves and shoots in pure populations were higher than in mixed populations, and so was the N content (although only significantly different to populations with <i>V. uliginosum</i>), pointing to a competition for N in mixed populations. Our results indicate that <i>V. myrtillus</i> competes for light with <i>R. ferrugineum</i> and for nutrients with both neighbours, but this competition does not affect its overall above-ground growth. Therefore, the interaction with co-occurring shrubs does not seem to affect the performance of <i>V. myrtillus</i> at treeline and thus, should not be considered a key driver on the dynamics of this species in the encroachment of subalpine grasslands.</p>
<p>Suggested Reviewers:</p>	<p>Rene van der Wal r.vanderwal@abdn.ac.uk His expertise on ecosystem function and diversity and the broad range of habitats he has worked in makes him a suitable reviewer for our work.</p> <p>Sarah Woodin s.woodin@abdn.ac.uk She carries out research on plant communities from ecophysiological aspects to vegetation processes. This wide range of expertise would be very useful for the revision of our work.</p> <p>Julia Wheeler juliawheeler@eco.umass.edu Her research has focused on dwarf shrubs in tundra communities, which are very similar to those we studied.</p> <p>Adrián Escudero adrian.escudero@urjc.es He is an expert on population and community ecology, and he has worked with high mountain plants.</p>

1 **Populations of *Vaccinium myrtillus* show similar structure and functioning under**
2 **different scenarios of coexistence at the Pyrenean treeline.**

3

4 **Short title:** *Vaccinium myrtillus* population structure and functioning at the treeline

5

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18 **Keywords:** biomass partition, competition, dwarf shrub, stable isotope composition, xylem
19 growth rings

20

21 **Abbreviations:** IRMS (isotope ratio mass spectrometry), NRE (nitrogen resorption
22 efficiency), NRP (nitrogen resorption proficiency), SPA (shoot photosynthetic area), TOM
23 (total organic matter), $\delta^{13}\text{C}$ (carbon isotope composition), $\delta^{15}\text{N}$ (nitrogen isotope composition)

24 **Abstract**

25 Plant-plant interactions are key drivers on modulating treeline dynamics. At the Pyrenean
26 treeline, the dwarf shrub *Vaccinium myrtillus* grows in pure populations or in mixed
27 populations with *Vaccinium uliginosum* or *Rhododendron ferrugineum*. They form sparse
28 shrub patches that colonize subalpine grasslands, having dramatic impacts on the structure
29 and functioning of these grassland communities. We investigated the role of the two co-
30 occurring shrubs as possible modulators of *V. myrtillus* population structure and performance
31 in the Central Pyrenees. We analysed age distribution, growth and functional parameters and
32 N and C cycling (i.e. N and C concentrations and isotope compositions, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of *V.*
33 *myrtillus* ramets under these three situations of coexistence. Ramet above-ground biomass and
34 population age structure did not differ between the three situations, but *V. myrtillus* growing
35 with *R. ferrugineum* reached greater volumes, a possible response of competition for light.
36 $\delta^{15}\text{N}$ values of *V. myrtillus* leaves and shoots in pure populations were higher than in mixed
37 populations, and so was the N content (although only significantly different to populations
38 with *V. uliginosum*), pointing to a competition for N in mixed populations. Our results
39 indicate that *V. myrtillus* competes for light with *R. ferrugineum* and for nutrients with both
40 neighbours, but this competition does not affect its overall above-ground growth. Therefore,
41 the interaction with co-occurring shrubs does not seem to affect the performance of *V.*
42 *myrtillus* at treeline and thus, should not be considered a key driver on the dynamics of this
43 species in the encroachment of subalpine grasslands.

44

45 **Introduction**

46 Plant-plant interactions represent one of the major selective forces driving population and
47 community dynamics (Callaway and Walker 1997). At the treeline ecotone, shrubs have been
48 identified as modulators of ecosystem dynamics (Batllori et al. 2009b; Grau et al. 2012).
49 However, the role of plant-plant interactions in shrub communities has often been disregarded
50 in favour of climate modulators (especially temperature; see the numerous warming
51 experiments carried out at treeline areas, e.g. Michelsen et al. 1996; Xu et al. 2009;
52 Kaarlejärvi et al. 2012; Anadon-Rosell et al. 2014). Shrubs can facilitate tree seedling survival
53 and recruitment because they can exert a nurse effect when tree species are in their most
54 vulnerable life stage (Gómez-Aparicio et al. 2008; Batllori et al. 2009b; Grau et al. 2012).
55 Moreover, interactions between woody species can have a key role in the encroachment
56 processes that have been reported during the last decades in alpine and Arctic tundra
57 ecosystems (Eldridge et al. 2011; Myers-Smith et al. 2011).

58 The temperature increase of the last decades in high mountain ecosystems (IPCC 2013)
59 and the progressive abandonment of traditional land-use in these areas (Tappeiner and
60 Cernusca 1993; Gellrich et al. 2008) have caused a densification of woody plants at European
61 alpine treelines (Stöcklin and Körner 1999; Camarero and Gutiérrez 2004; Kullman 2005;
62 Batllori and Gutiérrez 2008) and the re-colonization of abandoned pastures by shrubs (Didier
63 2001; Vicente-Serrano et al. 2004; Albert et al. 2008). This shrub encroachment, which is
64 predicted to increase in response to the higher temperatures forecasted for this century
65 (Walker et al. 2006; Meehl et al. 2007; IPCC 2013), plays an important role in the first stadia
66 of tree re-colonization at treeline (Tasser and Tappeiner 2002; Targetti et al. 2010; Ninot et al.
67 2011). Therefore, studies focusing on shrub species interactions at treeline can provide
68 essential understanding of the functioning of treeline ecosystem dynamics (Smith et al. 2003;
69 Batllori et al. 2009b; Grau et al. 2012; Llambí et al. 2013).

70 In the subalpine belt of the Pyrenees, *Vaccinium myrtillus* has a substantial role in the
71 transitional ecotone between *Pinus uncinata* forests and alpine grasslands (see Batllori et al.
72 2009a). In these areas it grows close to the highest altitudinal limit of its distribution (Bolòs et
73 al. 2005), where stressful conditions related to low temperatures, wind abrasion, early-season
74 frost and short growing seasons could lead to a prevalence of facilitative plant-plant
75 interactions (Batllori et al. 2009b; Fajardo and McIntire 2011). Numerous studies in alpine
76 and Arctic ecosystems have reported facilitative interactions between *Vaccinium myrtillus* and
77 co-occurring species (Maillette 1988; Shevtsova et al. 1995). At treeline in the Central
78 Pyrenees, *Vaccinium myrtillus* forms sparse patches together with the similarly-sized shrub
79 *Vaccinium uliginosum* ssp. *microphyllum* and the taller shrub *Rhododendron ferrugineum*.
80 These shrub communities have an important role on treeline dynamics due to their potential
81 for colonizing subalpine grasslands. However, the role of *Vaccinium uliginosum* and
82 *Rhododendron ferrugineum* as modulators of *Vaccinium myrtillus* population structure and
83 performance and, ultimately, the effects that these interactions can have on treeline dynamics
84 are poorly understood. Furthermore, studies on shrub interactions involving *Vaccinium*
85 species have usually considered neighbour shrubs of similar dimensions (Maillette 1988;
86 Shevtsova et al. 1995, 1997; Gerdol et al. 2000; Brancaleoni and Gerdol 2006), whereas the
87 effect of taller shrubs on these species remains poorly understood (but see Pornon et al. 2007).

88 Carbon and nitrogen isotope compositions (i.e. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of plant tissues can be
89 used to determine plant nutrient and/or water status. Natural abundance $\delta^{13}\text{C}$ values have been
90 used to assess plant water-use efficiency (Farquhar et al. 1982) and $\delta^{15}\text{N}$ values may provide
91 insight into the use of different sources of nitrogen (Ghashghaie et al. 2003, Tcherkez and
92 Hodges 2008), the niche partitioning for nitrogen acquisition (Pornon et al. 2007; Gundale et
93 al. 2012) and differential isotopic fractionation of nitrogen in response to different
94 mycorrhizal N uptake mechanisms (Emmertson et al. 2001). Moreover, carbon and nitrogen

95 mass-based concentrations can be used as a measure of nutrient availability and dynamics
96 (Aerts 1996; Killingbeck 1996; Palacio et al. 2007; Baptist et al. 2009; 2013; Muller et al.
97 2011; Vergutz et al. 2012). Previous studies have shown differences in the N-acquisition and
98 N-use strategies between *Vaccinium myrtillus* and coexisting species such as *Rhododendron*
99 *ferrugineum* or *Vaccinium vitis-idaea* (Pornon et al. 2007; Gundale et al. 2012). Nevertheless,
100 although studies on congeneric species have often shown that trait divergence and niche
101 separation are strategies for coexistence (Maillette et al. 1988; Vander Kloet and Hill 2000;
102 Beltrán et al. 2012; Gundale et al. 2012), this has not been assessed for the co-occurring *V.*
103 *myrtillus* and *V. uliginosum*.

104 We aimed to determine whether growth and survival of *V. myrtillus* ramets at the
105 treeline ecotone are affected by the coexistence with *Vaccinium uliginosum* ssp. *microphyllum*
106 and *Rhododendron ferrugineum* and to find out the primary plant-plant interactions driving
107 the performance of *V. myrtillus* in the area. To do so, we measured functional, growth and
108 demographical parameters using growth measures, isotopic analyses and dendroecological
109 techniques. We specifically tested the following hypotheses: (i) *V. myrtillus* will compete for
110 light with the taller shrub *R. ferrugineum*, and thus will present greater spread (vertically and
111 horizontally) when co-occurring with it; (ii) *R. ferrugineum* will exert a facilitative effect on
112 *V. myrtillus*, protecting it from environmental damage (e.g. wind damage and early-spring
113 frost) and this will translate into older, more vigorous ramets in these mixed populations; (iii)
114 growth and survival of *V. myrtillus* ramets from populations mixed with *V. uliginosum* will be
115 comparable to those from monospecific populations due to the structural similarity between
116 these two species (iv) *V. myrtillus* will not compete for nitrogen with the other two shrubs
117 owing to the putative different N-acquisition strategy from *R. ferrugineum* and to a niche
118 separation from the congeneric *V. uliginosum*, which will be reflected in a similar nutrient
119 content of ramets between different situations of coexistence.

120 **Materials and methods**

121 *Study area*

122 The study site is located at Eth Corrau des Machos, in the buffer zone of the Aigüestortes and
123 Estany de Sant Maurici National Park (Central Pyrenees, Catalonia, 31N 329, 472). Sampled
124 plots are located on an N-facing 10-25° steep slope at 2250 m a.s.l., slightly above the current
125 treeline in the area, but with some trees scattered above. Climatic data from a nearby location
126 (La Bonaigua, located 6.3 km away from the study site and at similar altitude) for the period
127 2007- 2012 are: mean annual precipitation 1154.9 mm and mean annual temperature 2.7 °C
128 (Meteorological Service of Catalonia, see detailed climatic data for the study period 2010-
129 2012 in Fig. 1).

130 At this site, vegetation is composed of *Festuca eskia* Ramond ex DC. and *Nardus*
131 *stricta* L. grasslands (Selino-Festucetum eskiae) mixed with patches of dwarf shrub heath
132 dominated by *Vaccinium myrtillus* L., *Vaccinium uliginosum* L. subsp. *microphyllum* (Lange)
133 Tolm. (*V. uliginosum* hereafter) and *Rhododendron ferrugineum* L. These communities are
134 considered as serial stages in the succession to mountain pine (*Pinus uncinata* Ramond ex
135 DC.) forests (Rhododendro-Pinetum uncinatae), which were formerly extensive in the area,
136 but are reduced at present due to anthropogenic deforestation.

137 *Experimental design*

138 In mid-September 2010 we established fifteen plots (20 x 20 cm) to assess the performance of
139 the deciduous dwarf shrub *Vaccinium myrtillus* in three different situations of coexistence:
140 five plots for populations of *V. myrtillus* without any other shrub (monospecific stands, M
141 populations), five for *V. myrtillus* co-occurring with *V. uliginosum* (mixed stands, U
142 populations) and five for *V. myrtillus* co-occurring with *Rhododendron ferrugineum* (mixed
143 stands, R populations). The size of the plots accounts for the relative small size of the stands.
144 The distance between two plots ranged from one to few meters (<20 m), depending on the

145 distribution of shrub stands along the study site but always ensuring that different plots
146 belonged to different patches. We carried out this study on a ramet basis due to the clonal
147 structure of this shrub, which consists of a horizontal network of subterranean rhizomes from
148 which arise aerial shoots (Ritchie 1956; Flower-Ellis 1971). We measured and clipped at
149 ground level all *V. myrtillus* ramets grounded within each plot boundaries, and we
150 subsequently stored them in sealed plastic bags kept in a portable cooler until we arrived at
151 the laboratory.

152 *Population structure, above-ground growth and plant performance*

153 To have an estimate of the ability of plants to compete for space at a population scale, we
154 calculated the volume of all *V. myrtillus* ramets present in each plot. To do so, we measured
155 their height and their canopy diameter (i.e. mean between the maximum and the minimum
156 canopy diameters) and estimated the theoretical volume occupied for each ramet as a canopy
157 cylinder ($V = \pi r^2 h$, Johnson et al. 1988). We defined four volumetric classes (<150, 150-599,
158 600-999, ≥ 1000 cm³) and calculated the percentage of ramets in each class.

159 To study above-ground biomass partition of individual ramets, we selected 12 ramets
160 per plot when possible (except for one M plot, which only had 11 ramets, and two R plots,
161 which only had 8 and 10 ramets), representative of the wide range of ramet sizes in the plots.
162 The following fractions were detached and counted: leaves, current-year shoots (formed in
163 2010, Sh1), one-year-old shoots (formed in 2009, Sh2), two-year-old shoots (formed in 2008,
164 Sh3) and main stem (> 3 years old). We identified different cohorts of shoots by the scars left
165 by bud scales after shoot elongation. Before drying, we cut 1.5 cm at the base of the stem of
166 each ramet for counting xylem growth rings to determine ramet age (see below). We dried all
167 the fractions at 70 °C for 72 h and weighed them to the nearest 0.001 g (with a Mettler Toledo
168 PB303 Delta Range scale). We corrected the weight of the main stems by adding the weight
169 of segments of similar dimensions to the part previously cut. We calculated the mean dry

170 mass per unit of Sh1, Sh2, Sh3 and main stem. For each ramet (except for ramets younger
171 than three years), we also measured the main stem diameter as the mean between the
172 maximum and minimum diameters measured at the base of the stem. We established four
173 stem diameter classes (0-1.49, 1.50-2.49, 2.50-3.49 and 3.50-4.50 mm) and calculated the
174 percentage of ramets in each class for each plot.

175 We randomly selected one of the 12 ramets described above in three plots of each
176 situation of coexistence and measured length and width of all shoots from the different
177 cohorts to calculate shoot photosynthetic area (SPA), assuming shoot surface area as that of a
178 tetrahedron. The greenness of the shoots gradually decreases as ramets age, therefore we only
179 considered the three last shoot cohorts (which show a clear green photosynthetic colour) for
180 SPA measurements. We carried out linear regressions between photosynthetic area and shoot
181 dry mass separately for each cohort and found positive significant correlations (Sh1: $R^2 =$
182 0.96 , $P < 0.001$; Sh2: $R^2 = 0.91$, $P < 0.001$; Sh3: $R^2 = 0.85$, $P < 0.001$, Fig. S1). Consequently,
183 we used the obtained regression equations to estimate the photosynthetic area of the rest of
184 shoots of all ramets.

185 *Population age structure*

186 The structure and growth of *V. myrtillus* ramets are dependent on age (Flower-Ellis 1971).
187 Thus, it is fundamental to know and consider ramet age when performing comparative studies
188 between *V. myrtillus* stands. To estimate the age of ramets and to identify differences in the
189 age structure of different populations, we made cross-sections of 20-25 μm thickness from the
190 basal segments of *V. myrtillus* stems using a sledge microtome. Sections were stained with
191 Safranin to emphasize the growth ring structure, subsequently rinsed with ethanol (75%) for
192 dehydration (Schweingruber and Poschold 2005, modified) and mounted in DPX. We counted
193 xylem growth rings under the microscope (Olympus CH2) and then calculated the percentage

194 of ramets in each age class (2-3, 4-6, 7-9, 10-12 year-old) for the three situations of
195 coexistence studied.

196 *C and N concentration and isotope composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)*

197 Leaves and current-year shoots from ramets harvested in 2010 were analysed for the
198 concentration and isotopic composition of C and N by pooling together the material of all
199 harvested ramets for each plot. However, since by the time of harvest (September 2010)
200 senescence had already started, we established another sampling period in August 2012 to
201 compare fully developed green leaves and leaves at senescence in the same populations. In
202 early August 2012 we collected *V. myrtillus* leaf and current-year shoot samples in fifteen
203 plots similar to those established in 2010, i.e. five plots for each situation of coexistence. We
204 sampled leaves and current-year shoots of five ramets per plot and pooled together the
205 material of these ramets for each plot separately, both for leaves and shoots. Thus, we had five
206 replicates for each situation of coexistence, sampling period and plant fraction. Samples were
207 dried at 60°C for 72 h, and subsamples were weighed in small tin capsules.

208 Samples were analysed to determine the carbon and nitrogen isotope composition
209 using a Flash 1112 Elemental Analyzer (Carbo Erba, Milan) coupled to an IRMS Delta C
210 isotope ratio mass spectrometer through a Conflo III Interface (Thermo-Finnigan, Germany).
211 Results of carbon isotope analyses are reported in per mille (‰) on the relative δ -scale as $\delta^{13}\text{C}$,
212 and refer to the international standard V-PDB (Vienna Pee Dee Belemnite) according to the
213 following equation:

214
$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \quad (\text{Eq.1})$$

215 where R is the $^{13}\text{C}/^{12}\text{C}$ ratio.

216 Carbon isotope discrimination ($\Delta^{13}\text{C}$) of shoot TOM (total organic matter) was
217 calculated from δ_a and δ_p (Farquhar et al. 1989) as:

$$218 \quad \Delta^{13}\text{C} = \frac{\delta_a - \delta_p}{\delta_p + 1} \quad (\text{Eq.2})$$

219 where a and p refer to air and plant, respectively.

220 Nitrogen results were also expressed in δ notation ($\delta^{15}\text{N}$) using international secondary
221 standards of known $^{15}\text{N}/^{14}\text{N}$ ratios (IAEA N₁ and IAEA N₂ ammonium sulphate and IAEA
222 NO₃ potassium nitrate) referred to N₂ in air:

$$223 \quad \delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \quad (\text{Eq.3})$$

224 where R is the $^{15}\text{N}/^{14}\text{N}$ ratio.

225 Nitrogen and carbon content were determined using an elemental analyzer (EA1108,
226 Series 1; Carbo Erba Instrumentazione, Milan, Italy).

227 We calculated the nitrogen resorption efficiency (NRE) on a mass basis (Killingbeck
228 1996) as:

$$229 \quad \text{NRE (\%)} = \left(\frac{N_g - N_s}{N_g} \right) \times 100 \quad (\text{Eq.4})$$

230 where N_g and N_s are the nitrogen content values in green leaves (August) and in
231 senescent leaves (September), respectively.

232 Moreover, we used the nitrogen content values in senescent leaves as an indicator of
233 nitrogen resorption proficiency (NRP) (Killingbeck 1996).

234 In August 2013, we collected air samples with a 50 ml syringe and kept them in 10 ml
235 vacutainers to analyze the $^{13}\text{CO}_2$ isotopic composition at the study site by gas-
236 chromatography-combustion-isotope ratio mass spectrometry (GC-C-IRMS) according to

237 Nogués et al. (2004). The $\delta^{13}\text{C}$ of CO_2 of the air at the site in the Pyrenees was ca. -10.91‰.
238 We also collected soil samples to determine soil nitrogen isotope composition at the study site
239 and analysed them following the same technique as mentioned above for plant material. Soil
240 $\delta^{15}\text{N}$ was ca. 7.33 ‰.

241 All the EA-IRMS and GC-C-IRMS analyses were performed at the Serveis Científico-
242 Tècnics of the University of Barcelona.

243 *Statistical Analyses*

244 We used linear mixed effects models fitted with the restricted maximum likelihood estimation
245 method (REML) to test the effects of the different scenarios of coexistence on the distribution
246 of *V. myrtillus* in volumetric and biomass classes and on the biomass partitioning, dry mass
247 per fraction, relative production of shoots in 2010 and SPA of each cohort of shoots. We
248 included the situation of coexistence as a fixed factor and plot as a random factor. To account
249 for the possible age effects on response variables, we included ramet age as a covariate in the
250 analyses of the effects of coexistence on individual ramet traits when it was significant, that is
251 for all variables except for the dry weight per Sh3 unit.

252 For the N and C concentrations and isotope compositions, we evaluated differences
253 between situations of coexistence, sampling period (August and September), plant fraction
254 (leaves and shoots) and their interaction with Type I analysis of variance using the linear
255 model function. For all statistical analyses we visually evaluated the assumptions of normality
256 and homoscedasticity of residuals (Zuur et al. 2009). We transformed response variables
257 when necessary to reach these assumptions and when transformations did not improve the
258 distribution of data we used the non-parametric Kruskal-Wallis test. Effects were considered
259 significant at $P < 0.05$ and marginally significant at $0.05 > P > 0.10$ to account for the
260 relatively low replication. When there were significant differences between situations of
261 coexistence, we performed Tukey HSD post hoc tests to determine which factor level means

262 differed significantly. To evaluate the dispersion of data, we calculated the coefficient of
263 variation (CV) of all variables in each situation of coexistence as the ratio of the standard
264 deviation and the mean. All analyses were performed with R 2.15.2 (R Core Team 2012),
265 using the nlme package (Pinheiro et al. 2008) for linear mixed effects models, the lattice
266 package (Sarkar 2008) for graphical evaluation of the assumptions of the models, the
267 multcomp package (Hothorn et al. 2008) for multiple comparisons on linear mixed effects
268 models and the agricolae package (de Mendiburu 2010) for multiple comparisons on simple
269 linear models.

270

271 **Results**

272 *Population structure, above-ground growth and performance*

273 The distribution of *V. myrtillus* ramets into the different volumetric classes was similar
274 between the three situations of coexistence, except for the percentage of ramets in the highest
275 volumetric class, which was higher in R than U populations. While 27% of the ramets from R
276 populations corresponded to the highest class, none of the ramets from U populations reached
277 the highest volumes (Kruskal-Wallis test, $H_2 = 6.8$, $P = 0.033$, Fig. 2). However, the average
278 height and the canopy width of ramets did not differ between the three situations of
279 coexistence ($F_{2,12} = 1.08$, $P = 0.37$ and Kruskal-Wallis test, $H_2 = 3.62$, $P = 0.1637$,
280 respectively).

281 Similarly, total above-ground standing biomass and above-ground biomass allocation
282 patterns of individual ramets did not differ between the three situations of coexistence ($F_{2,12} =$
283 1.92 , $P = 0.190$, Fig. 3). Within plant fractions, *V. myrtillus* allocated more biomass to main
284 stems (37% of the total biomass) followed by Sh1 (25%). Considering the dry mass per shoot
285 unit, the dry mass of Sh1 (13.20 ± 1.35 mg) was lower than that of the other two cohorts of
286 shoots (25.05 ± 3.35 mg and 40.48 ± 0.69 mg, respectively for Sh2 and Sh3), indicating the

287 progressive increase in biomass as shoots age. M populations allocated 52% more biomass to
288 Sh1 than the other two populations ($F_{2,12} = 4.79$, $P = 0.030$, Fig. 3) and the relative production
289 of current-year shoots in 2010 (dry mass Sh1/total biomass) was 6% higher in M populations
290 than in the other two situations of coexistence ($F_{2,12} = 9.27$, $P = 0.004$). The distribution in
291 stem diameter classes did not differ between the three situations ($P > 0.36$).

292 Shoot photosynthetic area (SPA) was similarly distributed across shoot cohorts, being
293 greater in Sh1 and followed by Sh2 and Sh3 for the three populations (Fig. 4). SPA of Sh1
294 was higher in M populations than in R and U populations ($F_{2,12} = 5.19$, $P = 0.024$, Fig. 4),
295 which is related to the larger biomass allocation to Sh1 in pure populations.

296 The coefficients of variation (CVs) of the variables studied ranged between 12.1%-
297 137.3% (M populations), 39.3%-223.6% (R populations) and 11.0%-183.0% (U populations)
298 (Table S1). R populations reached the greatest values, with 81% of the variables with a
299 standard deviation more than 50% of the mean, compared to 24% for M populations and 16%
300 for U populations. The distribution in the two highest volumetric classes and the distribution
301 in the highest and the lowest age and diameter classes were the variables showing the greatest
302 variability.

303 *Population age structure*

304 The distribution of *V. myrtillus* ramets in the different age classes did not differ between
305 situations of coexistence ($P > 0.24$, Fig. 5). For the three situations, most ramets were 4-6
306 year-old (55% for M and R populations and 39% for U populations), with the other age
307 classes being less represented. Ramet age was highly correlated to ramet stem diameter ($R^2 =$
308 0.30 , $P < 0.001$) and ramet total above-ground biomass ($R^2 = 0.28$, $P < 0.001$). M populations
309 had the greatest CVs in almost all the age classes (Table S1).

310 *C and N concentration and isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of leaves and new shoots*

311 We found significant differences in the C and N isotopic composition and N concentration of
312 leaves and shoots of *V. myrtillus* between situations of coexistence. $\delta^{13}\text{C}$ values of leaves and
313 shoots of *V. myrtillus* in pure populations and U populations were higher than those of ramets
314 from R populations ($F_{2,44} = 9.38$, $P < 0.001$, Fig. 6; see Table S3 for ^{13}C discrimination
315 values, $\Delta^{13}\text{C}$). $\delta^{13}\text{C}$ values of shoots were higher than values for leaves in the three situations
316 of coexistence ($F_{1,44} = 49.88$, $P < 0.001$) and values for August were higher than those of
317 September for both fractions and the three situations ($F_{1,44} = 0.43$, $P > 0.001$). We did not
318 find any significant effect of the interaction between situation of coexistence, sampling period
319 and plant fraction on the $\delta^{13}\text{C}$ of samples ($P > 0.64$). The carbon content of leaves and shoots
320 did not differ between situations of coexistence ($F_{2,44} = 0.53$, $P = 0.594$) or sampling periods
321 ($F_{1,44} = 2.46$, $P = 0.124$, Table 1), and it was higher in shoots than in leaves ($F_{2,44} = 54.47$, P
322 < 0.001).

323 $\delta^{15}\text{N}$ values of leaves and shoots of pure populations were higher than those of U and
324 R populations ($F_{2,44} = 13.72$, $P < 0.001$, Fig. 6) in both sampling periods. Values were higher
325 in August than in September ($F_{1,44} = 6.42$, $P = 0.015$), except for shoots of R populations,
326 which had higher values in September. The N content was higher in M populations than in U
327 populations ($F_{2,44} = 5.87$, $P < 0.005$). We found a significant sampling period x fraction
328 interaction ($F_{1,44} = 45.1$, $P < 0.001$, Table 1): values were significantly higher in August than
329 in September for leaves ($P < 0.001$, Tukey post hoc test) but shoots showed the opposite
330 trend, although it was not significant ($P = 0.998$, Tukey post hoc test). N concentrations did
331 not differ significantly between leaves and current-year shoots ($F_{1,44} = 1.86$, $P < 0.18$).

332 NRE mean values ranged between 34% (U populations) and 39% (R populations),
333 with M populations showing 37%, but these differences were not significant ($F_{2,10} = 0.11$, $P =$
334 0.896). Nitrogen resorption proficiency (NRP or $\%N_{\text{leaves}}$ in September) did not differ
335 between situations of coexistence either ($F_{2,10} = 0.59$, $P = 0.573$, Table 1).

336 The CVs for the $\delta^{13}\text{C}$ and the C content were very low (0.0%-4.2% and 0.2%-3.3%,
337 respectively) but they were higher for $\delta^{15}\text{N}$ and N content (8.4%-43.5% and 2.6%-18.8%,
338 respectively; Table S2).

339

340 **Discussion**

341 *Above-ground growth and performance*

342 The greater volume of *V. myrtillus* ramets growing with *R. ferrugineum* as compared to those
343 growing with *V. uliginosum* or in pure populations, suggests that *V. myrtillus* finds some
344 competition for light when growing with the taller shrub *R. ferrugineum*. *Vaccinium myrtillus*
345 can spread its shoots both laterally and upwards to occupy more space and intercept more
346 light, a plasticity that allows it to favourably compete for light (van Kleunen and Fisher 2001;
347 Mourelle et al. 2001; Callaway et al. 2003; Lepik et al. 2005). The observation that
348 differences in height and in canopy width were not significant across coexistence scenarios
349 suggests that, in the studied stands, it is a combination of a slight increase in both parameters
350 what allows *V. myrtillus* to show greater volumes when growing with *R. ferrugineum*.
351 However, this increased volume is not achieved through higher growth, as there are no
352 significant differences in the total above-ground biomass of *V. myrtillus* ramets found in the
353 different situations of coexistence. Although the relative production and biomass of *V.*
354 *myrtillus* current-year shoots were greater in ramets from pure stands on 2010, indicating
355 more favourable conditions for *V. myrtillus* growth in pure populations than in mixed
356 populations on that year, our data suggest that the coexistence with the other shrub species
357 does not affect accumulated above-ground growth of *V. myrtillus* in the study area. Different
358 results between 2010 and previous years might be due to interannual climate variability,
359 which is not accounted for in this study.

360 The photosynthetic potential of *V. myrtillus* shoots is especially important during the
361 cold season, when plants are leafless, because the green shoots of this species can
362 photosynthesize even under the snow cover (Körner 2003). SPA increased with shoot
363 biomass, and therefore, shoots of 2010 also had a greater photosynthetic area in ramets of
364 pure populations. However, apart from shoots of 2010, *V. myrtillus* SPA was similar across
365 populations, indicating a similar productive potential irrespective of the coexistence with *V.*
366 *uliginosum* and *R. ferrugineum*.

367 *Population age structure*

368 The lack of differences between the three situations of coexistence in the age structure of *V.*
369 *myrtillus* populations, together with the above-ground biomass results, implies that this
370 species does not encounter a different environment for its ramets establishment or survival
371 when growing with the other two shrubs than when growing in pure stands. We had expected
372 not to find differences in the population age structure between *V. myrtillus* pure stands and
373 stands with *V. uliginosum* because the effects of the intraspecific interaction between *V.*
374 *myrtillus* ramets would be functionally similar to the effects from the interspecific interaction
375 between ramets of the two *Vaccinium* species. However, our results indicate that we cannot
376 assume that the taller *R. ferrugineum* exerts any facilitative effect on *V. myrtillus* ramets
377 establishment and survival at our study site either. Grau et al. (2013) found that *R.*
378 *ferrugineum* reduced winter damage to tree seedlings at treeline sites in the Pyrenees. Also in
379 the Pyrenees, we observed that *R. ferrugineum* had some kind of nurse effect on *V. myrtillus*
380 in subalpine grasslands colonized by shrubs and in open shrublands, since the density of
381 ramets growing next to *R. ferrugineum* was higher than far from it (unpublished data).
382 Consequently, we expected to find older *V. myrtillus* ramets in plots with *R. ferrugineum*, but
383 such a nurse effect does not seem to occur at our study site.

384 All the populations analysed were formed by young ramets, the oldest ones being only
385 12 years old. This indicates we are dealing with patches where *V. myrtillus* has recently
386 established or patches where a high above-ground turnover maintains ramets at a young stage
387 by environmental constrictions or disturbance. The below-ground network of *V. myrtillus*
388 rhizomes can spread and expand clonally and thus, be much older than the above-ground
389 ramets (Flower-Ellis 1971). Therefore, only a long-term monitoring or a below-ground
390 dendrochronological survey could corroborate whether we are dealing with a recent
391 encroaching area where *V. myrtillus* could expand in the near future independently of the
392 absence or presence of *R. ferrugineum* and *V. uliginosum*.

393 *C and N concentration and isotope composition*

394 $\delta^{13}\text{C}$ values can be used as an estimate of the water use efficiency (WUE) of plants, with
395 lower $\delta^{13}\text{C}$ being indicative of lower WUE (Farquhar et al. 1982). Our results suggest that the
396 WUE of *V. myrtillus* is reduced in the presence of *R. ferrugineum*. Several studies have
397 reported lower values of $\delta^{13}\text{C}$ in leaves under shaded conditions than under full light (Gebauer
398 and Schulze 1991; Berry et al. 1997; Le Roux et al. 2001; Duursma and Marshall 2006;
399 Kranabetter et al. 2010). However, stomatal conductance is reduced under shade (Gross et al.
400 1996), leading to a lower discrimination against ^{13}C and higher $\delta^{13}\text{C}$ values in shaded plants.
401 The observed lower $\delta^{13}\text{C}$ values in ramets coexisting with *R. ferrugineum* are probably
402 explained by a greater difference in the assimilation rate between open and shady stands than
403 the difference in stomatal conductance between these two situations (Carelli et al. 1999).
404 When growing with *R. ferrugineum*, *V. myrtillus* encounters more shade, which probably
405 reduces its photosynthetic rate to a greater extent than the stomatal conductance (i.e. leading
406 to lower WUE values). As suggested by Forseth et al. (2001), the decreased WUE in *V.*
407 *myrtillus* growing with *R. ferrugineum* does not affect *V. myrtillus* growth because
408 temperature, vapour pressure deficit and transpiration rates may also be lower under the shade

409 of *R. ferrugineum*. The differences in the $\delta^{13}\text{C}$ values between sampling periods can be
410 explained by the decreasing photosynthetic efficiency at the end of the growing season, which
411 leads to higher isotope discrimination (Wang and Schjoerring 2012).

412 The lower nitrogen content and the lower $\delta^{15}\text{N}$ values of leaves and shoots in mixed
413 populations than in monospecific populations (although the nitrogen content was only
414 significantly different between M and U populations) suggest that, contrary to what we had
415 hypothesized, *V. myrtillus* encounters a deficit in available N when growing with *R.*
416 *ferrugineum* and *V. uliginosum* compared to pure stands (Olsrud et al. 2004; Craine et al.
417 2009). Wang and Schjoerring (2012) found a positive correlation between $\delta^{15}\text{N}$ and N
418 concentration in both green and senescent leaves of ryegrass from intensively managed fields
419 in Scotland. Craine et al. (2009) also found evidence that foliar $\delta^{15}\text{N}$ increased with increasing
420 N supply at a local and regional scale after reviewing data from 11,000 plants worldwide.
421 These results indicate that foliar $\delta^{15}\text{N}$ values and foliar N concentrations correlate and they
422 can both give information on the N availability. *Vaccinium myrtillus* and *R. ferrugineum* have
423 shown different N-acquisition strategies in an experiment in a subalpine community in the
424 French Pyrenees (Pornon et al. 2007), where *V. myrtillus* N uptake occurred early in the
425 growing season whereas *R. ferrugineum* showed a slower uptake rate, which was maintained
426 over the growing season. Moreover, a study on *V. myrtillus* and *V. vitis-idaea* in a boreal
427 shrub community (Gundale et al. 2012) showed that the removal of one shrub species did not
428 affect the isotopic signal of the other coexisting shrub, demonstrating that the niches of these
429 species were not affected by the presence of their neighbours. On the contrary, at our site *V.*
430 *myrtillus* seems to compete for nitrogen with *R. ferrugineum* and, especially, with *V.*
431 *uliginosum* but it can clearly counteract the effects of this competition and grow as vigorously
432 as in monospecific populations. Although the intraspecific competition for nitrogen may be
433 assumed between *V. myrtillus* ramets in pure stands, our results suggest that the interspecific

434 competition is higher. Further studies should be carried out to determine whether the lower
435 $\delta^{15}\text{N}$ values in leaves and shoots of *V. myrtillus* from mixed populations are due to higher ^{15}N
436 fractionation by mycorrhiza (Emmerton et al. 2001), to an increased proportion of N obtained
437 by mycorrhiza (Hobbie et al. 2000), or to the use of different nitrogen sources (Michelsen et
438 al. 1998) as a result of the competition with the other shrub species. Finally, the lower N
439 content in U populations than in pure populations (and although not significant, also lower in
440 R populations than in pure populations), suggest that the leaf quality of *V. myrtillus* is affected
441 by the presence of *V. uliginosum*. This is probably explained by the competition for nitrogen
442 between them, which limits the amount of nitrogen that *V. myrtillus* ramets can invest in their
443 leaves when coexisting with *V. uliginosum*. Alternatively, factors derived from
444 microtopography (such as snow cover or soil quality) could partly explain the differences in
445 the nitrogen content of *V. myrtillus* tissues between situations of coexistence.

446 The resorption of nutrients that takes place prior to senescence in deciduous species
447 (Killingbeck 1996) is reflected in *V. myrtillus* by the lower values of leaf nitrogen content in
448 September than in August. Moreover, the higher values of shoot nitrogen content in
449 September than in August indicate that N is transported from leaves to shoots before leaf
450 shedding. Leaf and shoot $\delta^{15}\text{N}$ values were lower in September, which might be explained by
451 an isotopic discrimination associated to nitrogen resorption. Previous studies have found no
452 evidence of negative nitrogen isotope discrimination during the resorption period (Kolb and
453 Evans 2002), but it has been found in processes such as nitrogen reallocation or loss (Evans
454 2001; Dawson et al. 2002; Kolb and Evans 2002), which suggests that a negative
455 discrimination associated to resorption could occur. Although the nitrogen content of *V.*
456 *myrtillus* leaves and shoots was reduced in the presence of *V. uliginosum*, the nitrogen
457 resorption efficiency (NRE) and proficiency (NRP) were not altered by the presence of any of
458 the other two shrub species.

459 *Concluding remarks*

460 We did not find evidence that the performance of *V. myrtillus* at our study site is affected by
461 the presence of *Rhododendron ferrugineum* or *Vaccinium uliginosum*. Although *Vaccinium*
462 *myrtillus* seems to compete for nitrogen with both species, it can counterbalance these
463 competition effects without compromising its growth and survival. This is especially
464 important to understand and predict landscape dynamics at treeline: the possible expansion of
465 *V. myrtillus* at this treeline site is independent of the presence of *V. uliginosum* and *R.*
466 *ferrugineum* and is more related to other biotic interactions and climate factors.

467

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728 **Figure legends**

729 **Fig. 1** Monthly mean temperature (°C) and precipitation (mm) from 2010 to 2012 at La
730 Bonaigua Station (Meteorological Service of Catalonia), located at 2266 m a.s.l., 6.3 km from
731 the study site.

732

733 **Fig. 2** Percentage of *V. myrtillus* ramets in each volumetric class for the three situations of
734 coexistence studied. The asterisk shows significant differences between situations of
735 coexistence ($P < 0.05$), referred to the highest volumetric class between R populations and U
736 populations. Data are means + 1 SE, $n = 5$. M: monospecific populations of *V. myrtillus*, R:
737 stands of *V. myrtillus* mixed with *R. ferrugineum*, U: stands of *V. myrtillus* mixed with *V.*
738 *uliginosum*

739

740 **Fig. 3** Biomass allocation in *V. myrtillus* ramets for the three situations of coexistence studied.
741 The asterisk shows significant differences between situations of coexistence ($P < 0.05$),
742 referred to Sh1 between M populations and R and U. Data are means + 1 SE, $n = 5$. M:
743 monospecific populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R.*
744 *ferrugineum*, U: stands of *V. myrtillus* mixed with *V. uliginosum*. Sh1: current-year shoots,
745 Sh2: one-year-old shoots, Sh3: two-year-old shoots.

746

747 **Fig. 4** Shoot photosynthetic area of *V. myrtillus* ramets in the three situations of coexistence
748 studied. The asterisk shows significant differences between situations of coexistence ($P <$
749 0.05), referred to Sh1 between M populations and R and U. Data are means + 1 SE, $n = 5$. M:
750 monospecific populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R.*
751 *ferrugineum*, U: stands of *V. myrtillus* mixed with *V. uliginosum*. Sh1: current-year shoots,
752 Sh2: one-year-old shoots, Sh3: two-year-old shoots.

753

754 **Fig. 5** Percentage of *V. myrtillus* ramets in each age class. Differences between situations of
755 coexistence were not significant at $\alpha = 0.05$. Data are means + 1 SE, $n = 5$. M: monospecific
756 populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R. ferrugineum*, U: stands of
757 *V. myrtillus* mixed with *V. uliginosum*.

758

759 **Fig. 6** ^{13}C and ^{15}N isotopic composition (i.e. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of leaves and new twigs of 2012
760 sampled in August and September. Different letters indicate significant differences between

761 situations of coexistence, sampling period or plant fraction ($P < 0.05$). Data are means - 1 SE,
762 $n = 5$. M: monospecific populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R.*
763 *ferrugineum*, U: stands of *V. myrtillus* mixed with *V. uliginosum*. The $\delta^{13}\text{C}$ of air CO_2 was ca.
764 -10.91‰ and the $\delta^{15}\text{N}$ of soil was ca. 7.33‰ .

Figure 1

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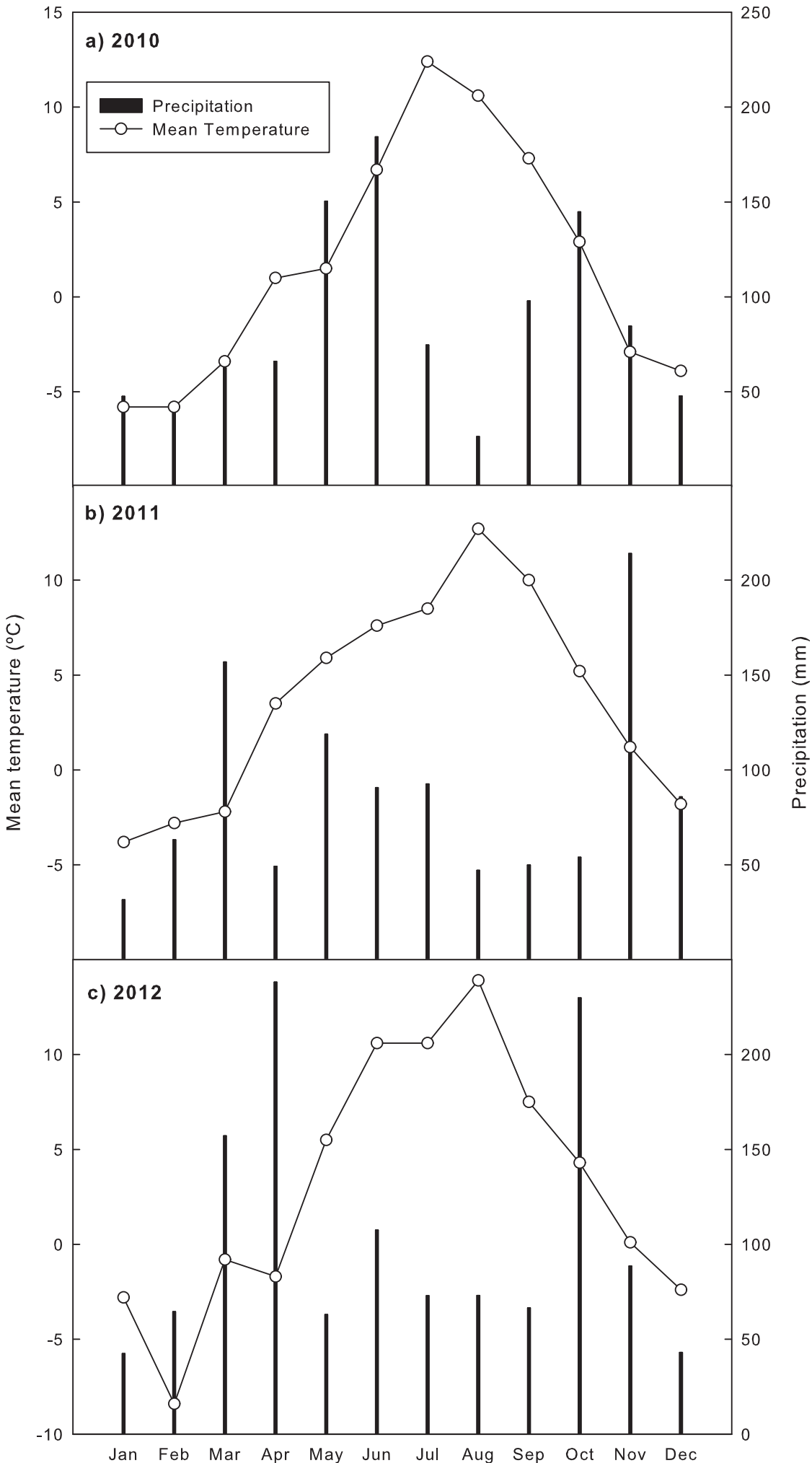


Figure 2

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Figure 3

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Figure 4

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Figure 5

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Figure 6

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Table 1. Data on the C and N content for leaves and current-year shoots of *V. myrtillus* sampled in August and September in the different situations of coexistence. Values represent means of the five replicates for each situation of coexistence \pm 1 SE.

Coexistence	Sampling period	C _{leaves} (%)	C _{shoots} (%)	N _{leaves} (%)	N _{shoots} (%)
M	August	50.08 \pm 0.73	52.5 \pm 0.04	2.21 \pm 0.19	1.67 \pm 0.06
	September	51.09 \pm 0.29	51.56 \pm 0.53	1.38 \pm 0.18	1.69 \pm 0.04
R	August	49.01 \pm 0.40	52.43 \pm 0.49	1.9 \pm 0.08	1.48 \pm 0.04
	September	51.03 \pm 0.23	52.21 \pm 0.24	1.16 \pm 0.16	1.59 \pm 0.14
U	August	50.28 \pm 0.33	52.07 \pm 0.48	1.83 \pm 0.07	1.36 \pm 0.08
	September	50.97 \pm 0.19	52.05 \pm 0.22	1.19 \pm 0.11	1.57 \pm 0.07

M: monospecific populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R. ferrugineum*,

U: stands of *V. myrtillus* mixed with *V. uliginosum*.

Supporting information

Table S1. Coefficients of variation (%) for the above-ground growth, performance and age parameters studied.

	Population		
	M	R	U
Volumes			
<150 cm ³	23.63	67.26	18.56
150-599 cm ³	24.56	65.90	41.43
600-999 cm ³	66.95	74.46	182.96
≥ 1000 cm ³	126.46	131.80	NA
Total biomass	22.55	83.35	24.37
Biomass partition			
Sh1	19.57	66.59	16.45
Sh2	19.71	78.31	18.09
Sh3	24.13	81.46	24.32
Main stem	33.82	92.37	48.91
Dry weight per unit			
Sh1	38.24	43.06	35.30
Sh2	15.29	41.68	33.43
Sh3	12.12	75.87	33.62
Main stem	33.82	92.37	48.91
DW Sh1/DW Total	6.79	11.77	3.99
SPA			
Sh1	18.49	61.51	14.99
Sh2	20.41	82.08	19.32
Sh3	20.53	69.20	11.00
Diameter classes			
0-1.49 mm	114.28	77.55	98.09
1.50-2.49 mm	39.17	39.28	21.47
2.50-3.49 mm	61.56	78.60	83.53
3.50-4.05 mm	137.25	223.61	NA
Age	17.63	16.82	7.60
Age classes			
2-3 years	120.44	78.18	50.21
4-6 years	37.24	26.44	33.25
7-9 years	51.32	52.08	29.27
10-12 years	155.08	95.83	137.15

M: monospecific populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R. ferrugineum*, U: stands of *V. myrtillus* mixed with *V. uliginosum*. Sh1: current-year shoots, Sh2: one-year-old shoots, Sh3: two-year-old shoots. DW: dry weight.

Table S2. Coefficients of variation (%) for the nitrogen and carbon parameters studied.

	Population		
	M	R	U
$\delta^{13}\text{C}$			
Leaves August	2.06	-1.59	-1.15
Branches August	4.21	-1.45	-2.28
Leaves September	0.69	-0.01	-0.73
Branches September	1.55	-1.57	-1.52
$\delta^{15}\text{N}$			
Leaves August	38.04	-36.57	-8.37
Branches August	43.45	-33.19	-23.00
Leaves September	23.84	-19.72	-17.37
Branches September	10.36	-13.36	-13.50
C content			
Leaves August	3.25	1.85	1.48
Branches August	0.18	2.10	2.06
Leaves September	0.57	0.44	0.38
Branches September	1.04	0.46	0.42
N content			
Leaves August	18.77	8.88	8.49
Branches August	7.95	5.86	13.85
Leaves September	12.80	13.59	9.56
Branches September	2.59	8.81	4.32
NRE	43.97	21.67	49.04

M: monospecific populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R. ferrugineum*, U: stands of *V. myrtillus* mixed with *V. uliginosum*.

Table S3. $\delta^{13}\text{C}$ and $\Delta^{13}\text{C}$ of the leaf and shoot TOM (total organic matter) for the three situations of coexistence studied. M: monospecific populations of *V. myrtillus*, R: stands of *V. myrtillus* mixed with *R. ferrugineum*, U: stands of *V. myrtillus* mixed with *V. uliginosum*. Values represent means \pm 1 SE ($n = 5$). The $\delta^{13}\text{C}$ of the CO_2 was -10.91‰ .

Population	Fraction	Sampling period	$\delta^{13}\text{C}$ (‰)	$\Delta^{13}\text{C}$
M	Leaf	August	-28.62 ± 0.26	17.71 ± 0.26
		September	-29.26 ± 0.20	18.35 ± 0.20
	Shoot	August	-27.58 ± 0.52	16.67 ± 0.51
		September	-27.79 ± 0.43	16.88 ± 0.43
R	Leaf	August	-29.48 ± 0.21	18.57 ± 0.21
		September	-30.45 ± 0.00	19.54 ± 0.00
	Shoot	August	-28.07 ± 0.18	17.16 ± 0.18
		September	-29.52 ± 0.46	18.61 ± 0.46
U	Leaf	August	-28.87 ± 0.15	17.96 ± 0.15
		September	-29.32 ± 0.21	18.41 ± 0.21
	Shoot	August	-27.62 ± 0.28	16.71 ± 0.28
		September	-27.84 ± 0.42	16.93 ± 0.42

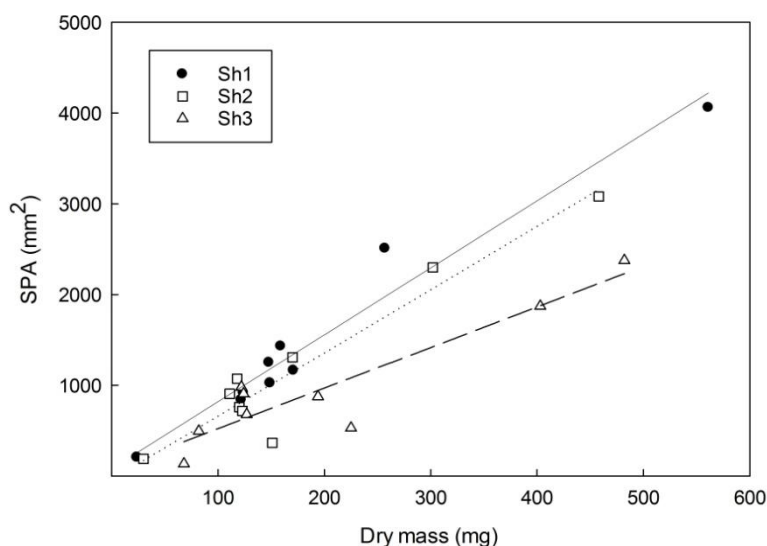


Figure S1. Correlations between shoot photosynthetic area (SPA, mm^2) and shoot dry mass (mg) of current-year shoots (Sh1), one-year-old shoots (Sh2) and two-year-old shoots (Sh3) of *V. myrtillus*. We used the obtained regression equations to estimate SPA of the rest of the study ramets: $y = 7.38x + 79.66$ (Sh1), $y = 6.98x - 39.46$ (Sh2), $y = 4.48x + 73.26$ (Sh3).