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**Climate and vegetation structure determine plant diversity in *Quercus*
ilex woodlands along an aridity and human-use gradient in Northern
Algeria**

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26 ABSTRACT

27 We studied the influence of environmental factors relating to climate, soil and
28 vegetation cover on total species richness, species richness of different life-forms and
29 species composition of plant communities occurring in *Quercus ilex* woodlands, across
30 a 450-km long transect in Northern Algeria constituting a gradient of aridity and human
31 use. We sampled vegetation and collected environmental data in 81 10 × 10 m² plots in
32 five zones representing the largest *Q. ilex* woodlands throughout the study area,
33 analysing them within an *a-priori* hypothesis framework with the use of Path Analysis.
34 Changes in plant diversity were mainly influenced by environmental factors related to
35 precipitation and temperature regimes, as well as by total plant cover. In particular,
36 changes in species composition were determined by factors associated with the
37 temperature regime through their influence on both woody and annual herbaceous plant
38 richness, and by factors related to the precipitation regime through their influence on
39 perennial herbaceous plant richness, likely due to the differential tolerances of these
40 functional groups to cold and water stress. Our results emphasize the importance of
41 differences in environmental adaptability of the most important life-forms with regard
42 to explaining compositional change (beta diversity) along aridity gradients, and the
43 mediator role of total plant cover in relation to the effects of soil conditions on plant
44 diversity.

45

46 *Keywords:* Species composition; species richness; plant life-forms; precipitation
47 regime; temperature regime; total plant cover; path analysis.

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50

51 **Introduction**

52 Explaining the relationships between diversity of vascular plant communities and
53 environmental factors across broad-scale geographical gradients is of particular interest
54 for ecological research (Pausas and Austin, 2001). There has been an increasing amount
55 of studies on this topic over the last few decades (Ferrer-Castán and Vetaas, 2005;
56 Vetaas and Ferrer-Castán, 2008; Field et al., 2009), a fact that might help to assess the
57 main processes determining the assemblage of plant communities (Lortie et al., 2004),
58 and the prevalence of negative (i.e. intra- and inter-specific competition) and positive
59 (i.e. facilitation) interactions thereupon (Bertness and Callaway, 1994). These studies
60 are often linked to applied issues such as land management and predictions related to
61 climate change (Whittaker et al., 2007).

62 Plant diversity presents different components and can be measured in different
63 ways, but it is usually expressed as species richness at a given location (alpha diversity)
64 and as the rate of compositional change along habitat gradients (beta diversity) (Purvis
65 and Hector, 2000; Rey-Benayas and Scheiner, 2002). Over any large region, vascular
66 plant diversity is primarily governed by abiotic factors associated with climate, in
67 particular to the water (precipitation) and energy (temperature) regimes (O'Brien,
68 2006). Factors related to the precipitation regime are the strongest predictors of plant
69 diversity patterns in the warm temperate zones of the world (Hawkins et al., 2003), in
70 Southern Europe (Whittaker et al., 2007), and along shorter environmental gradients in
71 Mediterranean-climate areas (Kutiel et al., 2000). In areas where water is a limiting
72 factor, plant diversity is also determined by factors relating to the temperature regime,
73 showing a decrease with higher temperatures (Whittaker et al., 2007). Changes in plant
74 diversity are also affected by abiotic factors related to edaphic conditions such as soil
75 fertility (Cowling, 1996), texture and moisture (Rey-Benayas and Scheiner, 2002).

76 Abiotic factors relating to climate and soil conditions that determine changes in plant
77 diversity across environmental gradients are usually closely interrelated (Purvis and
78 Hector, 2000; Pausas and Austin, 2001). Thus, soil fertility is affected by precipitation
79 and temperature (Sarah, 2004) and by soil moisture and texture (Sardans and Peñuelas,
80 2007), whereas soil moisture is strongly influenced by precipitation, temperature and
81 soil texture (Rey-Benayas et al., 2004).

82 Changes in vascular plant diversity are also affected by biotic factors associated
83 with vegetation structure, such as total plant cover, which can be considered as a
84 correlate for interactions between woody and herbaceous plants (North et al., 2005). In
85 the Mediterranean-climate regions of the world total plant cover may enhance
86 recruitment of annual herbaceous plants by alleviating water and irradiance stress in the
87 understorey (Atkinson and Gleeson, 2004), and total plant cover commonly shows
88 strong and positive relationships with plant diversity (Torras et al., 2008). Total plant
89 cover depends on precipitation and temperature (Torras et al., 2008), and in
90 Mediterranean regions it is limited by soil texture (Le Houerou, 2001), moisture and
91 fertility (Moreno-de-las-Heras et al., 2009). Total plant cover plays also an important
92 role in mediating relationships between soil conditions and plant diversity (Ehrenfeld et
93 al., 2005), and can be greatly determined by human activities such as wood extraction
94 and grazing by domestic herbivores (De Bello et al., 2005).

95 Since relationships between vascular plant diversity and ecosystem processes
96 depend to a great extent on the presence and dominance of different functional groups
97 (Chapin, 2003; Berendse, 2005; Lavorel et al., 2007), relationships between plant
98 diversity and environment across broad-scale geographical gradients are easier to
99 interpret on considering changes in species richness of functional types, and growth or
100 life forms are commonly used for this purpose (Pausas and Austin, 2001). Woody and

101 herbaceous species are characterized by different kinds of adaptations to water
102 limitation and consequently, they show differential responses to regional variations in
103 precipitation (Kadmon and Danin 1999). Woody plants, with their long and extensive
104 root systems, make use of the water stored in the deeper soil layers (Lu et al., 2006). In
105 the Mediterranean basin they may even appear in relatively dry areas (Bonet and Pausas
106 2004), and changes in species richness of this life form across environmental gradients
107 are determined by factors related to the temperature regime rather than to precipitation
108 (Field et al. 2005; Whittaker et al., 2007; Vetaas and Ferrer-Castán, 2008). Conversely,
109 herbaceous plants can only utilize the transient water stored in the topsoil, synchronic
110 with spatial (i.e. topography and texture) and temporal (i.e. precipitation) pulses (Lu et
111 al., 2006) and their presence in a specific area is highly dependent on soil conditions, in
112 particular soil moisture (Sher et al., 2004; North et al., 2005). In semi-arid areas, annual
113 herbaceous plant richness commonly exhibits a large spatial and temporal variability,
114 although it usually shows an increase in places where total plant cover is higher
115 (Holzapfel et al., 2006).

116 The effects of climatic factors upon changes in species richness and composition of
117 vascular plants along broad-scale geographical gradients have been widely evaluated
118 (Rey-Benayas and Scheiner, 2002; Vetaas and Ferrer-Castán, 2008). The same applies
119 to the effects of abiotic factors related to soil conditions upon changes in total plant
120 richness (Maestre, 2004) and in richness of the main functional types (Kadmon and
121 Danin, 1999; Kutiel et al., 2000; Lu et al., 2006) at regional scales. There is, however, a
122 lack of studies focusing both on abiotic and biotic factors as determinants of changes in
123 species richness and composition and on the plant richness of major life-forms,
124 considering the interrelations between factors (Lortie et al., 2004).

125 In this study, we analyze the influence of environmental factors on plant diversity of
126 holm-oak (*Quercus ilex* sp. *rotundifolia*, L.) woodlands along an aridity gradient
127 overlaying a human-use gradient in Northern Algeria. We focused on this area because
128 it includes a smooth biome transition between Mediterranean and arid climatic
129 conditions and because biome transition zones are the areas most sensitive to directional
130 changes in climate (di Castri et al., 1988). As *Q. ilex* woodland constitutes the most
131 widely distributed vegetation type across the study area, it enables comparisons among
132 relatively distant sites. We aim to explain the relative importance of factors related to
133 the precipitation and temperature regimes, soil conditions and total plant cover with
134 regard to determining changes in total species richness and composition, and species
135 richness of woody, perennial herbaceous and annual herbaceous plants, and we attempt
136 to assess how these factors interrelate. Specifically, we hypothesized that: (i) Changes
137 in total plant richness and species composition will be primarily determined by factors
138 associated with the precipitation and temperature regimes, respectively. (ii) Changes in
139 woody plant richness will be mainly determined by factors related to the temperature
140 regime, whereas changes in herbaceous plant richness will be determined principally by
141 factors related to the precipitation regime. In particular, annuals will be positively
142 affected by soil moisture and by total plant cover. (iii) Factors related to soil conditions
143 will determine changes in total plant richness and species composition through their
144 effects on total plant cover. Verification of these predictions will provide clues to the
145 processes determining plant diversity across areas representing the transition between
146 humid and semi-arid Mediterranean climate conditions, and in relation to plausible
147 changes in the Mediterranean plant communities of Northern Africa under regional
148 predictions of climate change.

149

150 **Materials and methods**

151 *Study area*

152 The study was conducted along a latitudinal transect in Northern Algeria (36° 36'-
153 34° N and 2°- 3° 37'E), which is 450 km long and encompasses the transition between
154 Mediterranean and arid climate conditions (Fig. 1). In this area, *Q. ilex* woodlands occur
155 mostly on steep and northern-oriented slopes within a broad altitudinal range (300-2200
156 m a.s.l), but they have a clear preference for higher altitudes in the southernmost areas
157 (Dahmani-Megrerouche, 2002). As many other types of vegetation in Northern Africa,
158 they are suffering from increasingly intense and frequent human-induced disturbances
159 such as firewood extraction and grazing (Vogiatzakis et al., 2006).

160 Along this transect we selected the largest areas of *Q. ilex* woodlands, which were
161 grouped into five zones, namely Blida, Miliana, Berrouaghia, Teniet-el-Had and Aflou.
162 These zones presented a broad array of climatic conditions within the Mediterranean
163 domain (Table 1, Fig. 1) as well as different intensities of human use (Table 2). Blida
164 and Miliana show mostly sub-humid/warm climatic conditions with some humid/warm
165 locations. They differed in human-use intensity, which was greater in Miliana than in
166 Blida because of the higher cattle and livestock load. Of the five zones, Blida comprised
167 the largest area of *Quercus ilex* woodlands. Berrouaghia and Teniet-el-Had, show sub-
168 humid/cold and dry/cold climatic conditions, respectively. Both zones present a higher
169 livestock load than Blida and Miliana. Berrouaghia also harbours the largest human
170 population in the study region. Aflou exhibits very dry/cold climatic conditions and has
171 the largest livestock load. The Aflou *Quercus ilex* woodlands covered the smallest area
172 of the five zones. In general terms, heading south along the transect precipitation and
173 mean minimum temperatures show a decrease, and livestock load increases.

174

175 ***Field sampling***

176 We sampled a total of 81 10 ×10 m² plots. The number of plots per zone (28 in
177 Blida, 9 in Miliana, 18 in Berrouaghia, 11 in Theniet-el-Had and 15 in Aflou) referred
178 to the total area occupied by *Quercus ilex* woodlands (Table 2). Miliana was an
179 exception, as proportionately fewer plots were surveyed due to the fact that access was
180 restricted to much of the *Q. ilex* woodland in this zone. Field sampling was performed
181 in spring (April-May). We sampled most plots in 1990, but five were sampled in 1991
182 (all in Blida) and 15 (ten in Blida and five in Miliana) in 1999, due to security problems.
183 In each plot, we collected data on the number of species and species composition. All
184 species were classified according to three relevant life-forms; woody, perennial
185 herbaceous and annual herbaceous plants.

186 For each plot, we recorded data on environmental factors with a direct impact on
187 physiological processes and which thus limit the spatial distribution of the plants
188 (Pausas and Austin, 2001). We obtained climate data from records of the nearest
189 meteorological stations (Table 1): mean annual precipitation (hereafter MAP, mm),
190 mean quotient of monthly precipitation and mean minimum temperature of the coldest
191 month (hereafter MTC, °C). We obtained soil data by taking three 20-cm deep soil cores
192 in each plot; the cores were mixed into a single composite soil sample that was analyzed
193 after being dried, crushed and passed through a 2-mm sieve. We measured soil water
194 content at three soil water potential values (Pf2.5, Pf3 and Pf4.2, at 0.33, 1 and 13 bar,
195 respectively) by means of a pressure membrane, before and after drying soil samples in
196 an air oven at 105 °C. Soil fertility variables included soil organic matter (calculated
197 from organic C with Anne's method), total N (calculated by means of Kjeldhal's
198 method), exchangeable Ca, Mg, K and Na (calculated by extraction with 1 M
199 ammonium acetate at pH = 7.0), effective cationic exchange capacity (hereafter CEC;

200 calculated with Metson's method), percent total and active limestone (calculated by
201 extraction of calcium carbonate with ammonium oxalate), and pH (calculated in a 1:2.5
202 suspension with 1 M KCl). Soil texture variables included clay, silt and sand
203 proportions in each plot, proportions of the most abundant types of clay, namely
204 kaollinite, chlorite and illite, and proportions of fine- and coarse-grained sand. Total
205 plant cover (hereafter TPC, %) was calculated by means of direct visual estimation.
206 Data on topography-related factors such as latitude and longitude, elevation (m a.s.l),
207 slope (%), and aspect (N, S, W and E) were measured with a GPS and a clinometer.
208 However, we did not include these factors in our analyses because they were surrogates
209 of other important variables affecting plant growth (Pausas and Austin, 2001).
210 Nomenclature of plant species follows Maire (1982) and Castroviejo et al. (2009).

211

212 ***Data analysis***

213 To determine whether there were significant differences in species composition
214 among the five zones, we applied an Analysis of Similarities (ANOSIM) (Clarke, 1993)
215 to the presence-absence (plots x species) matrix, using 99,999 Monte-Carlo
216 permutations. To determine if there were significant differences between zones for all
217 environmental factors considered, we performed one-way ANOVA and *post-hoc*
218 Tukey's tests.

219 To identify the major gradients of change in species composition and their
220 explanatory environmental factors, we followed a two-step procedure. First, we selected
221 the most independent and meaningful environmental factors by means of a Pearson's
222 product-moment correlation considering all factors and a Principal Component Analysis
223 (PCA) for each group of climatic, soil-moisture, soil-fertility and soil-texture factors
224 separately. As we detected highly correlated factors within these groups of variables

225 (Pearson's $r > 0.6$), we selected those with the highest factor loadings (> 0.5) on the first
226 PCA axis, in each group of factors. Among the factors associated with temperature
227 regime, soil moisture, fertility and texture, we selected MAP, Pf3, CEC and proportion
228 of sand, respectively (Appendix B). Secondly, we used a Non-metric Multidimensional
229 Scaling (NMDS) ordination analysis to visualize floristic gradients and interpret them
230 with respect to the environmental factors selected. As changes in species richness and
231 composition among plots can be influenced by their spatial locations (namely elevation
232 and latitude) across the study area, we partitioned the variation of species composition
233 into several components, namely pure environmental, pure spatial, environmental
234 component of spatial influence and spatial component of environmental influence,
235 through a sequence of analyses (Borcard et al. 1992). We determined the general
236 variance in species composition by performing a Detrended Correspondence Analysis
237 (DCA), and the environmental and spatial components of this variance by performing
238 two Canonical Correspondence Analyses (CCA), constrained by the environmental
239 factors previously selected by the PCA (CCA1) and the spatial data (i.e. latitude,
240 longitude and elevation) (CCA2), respectively. We determined the environmental
241 component of spatial influence and the spatial component of environmental influence by
242 conducting two partial CCA (pCCA), one constrained by the environmental factors and
243 using the best spatial predictors detected in CCA1 as covariables (pCCA1), and the
244 other constrained by the spatial data and using the best environmental predictors
245 detected in the CCA2 as covariables (pCCA2). In all CCA and pCCA analyses, we
246 evaluated the significance of the first ordination axis by performing Monte Carlo tests
247 with 999 permutations.

248 To assess the relative importance of the selected environmental factors in
249 determining species composition, total species richness and species richness of life-

250 forms, and to investigate their interrelationships, we used Path Analysis (Shipley, 1997).
251 Path Analysis is a technique especially developed to test a model of relationships among
252 variables (path diagram) and proposed by the researcher based on *a-priori* knowledge
253 (Malaeb et al., 2000). The results of a Path Analysis yield several goodness-of-fit
254 indices of the overall model, unexplained variances for the “focus” (pure dependent)
255 and “endogenous” (which can act either as independent or dependent) variables and
256 standardized partial regression coefficients for each relationship in the model. Low
257 unexplained variances for the “focus” variable imply that the equations are considering
258 relevant explanatory variables (Iriundo et al., 2003). Each standardized partial
259 regression coefficient has a sign that indicates the direction of the relationship, a
260 magnitude value (0-1) which indicates the degree to which the independent variable
261 directly influences the dependent variable of the analyzed relationship with all other
262 variables held constant, and a significance value that is assessed by means of a
263 multivariate Wald’s test (Shipley, 1997).

264 We considered as focus variables of the tested relationships total plant richness,
265 woody, perennial herbaceous and annual herbaceous plant richness, and species
266 composition. The latter was measured as coordinates of plots in the first dimension of
267 the NMDS. As independent variables, and in order to avoid problems related with the
268 presence of strongly correlated factors (i.e. collinearity; Petraitis et al. 1996), we
269 considered the factors previously selected at the Pearson’s product-moment correlation
270 and PCA; mean annual precipitation, soil water content (Pf3), effective cationic
271 exchange capacity, proportion of sand and total plant cover (Appendix B). We proposed
272 an initial path diagram (Model A in Fig. 2), and in order to make it simpler and improve
273 its goodness-of-fit, we proposed alternative path diagrams which sequentially excluded
274 those paths showing the lowest non-significant standardized partial regression

275 coefficients (Petraitis et al. 1996), and were labelled models B, C, D, E, F and G. In all
276 models, we considered residual correlations between the exogenous variables and
277 unexplained variances for each of the focus variables (Fig. 2). We evaluated the
278 Goodness-of-fit of all models by means of a “Chi-square” test (χ^2 statistic), and
279 calculated the Bentler and Bonnet’s normed-fit and Goodness-of-fit indices, NFI and
280 GFI, respectively, which are specially recommended when the number of observations
281 is <100 (Iriondo et al., 2003). A high and non-significant χ^2 statistic and values of NFI
282 and GFI indices > 0.9 indicate an acceptable fit of the models. As we provide sound
283 theoretical justifications for maintaining all the paths represented in the initial model,
284 we only kept any of the alternative models based on the principle of parsimony when
285 their χ^2 values remained relatively low despite their increasingly higher number of
286 degrees-of-freedom (Malaeb et al., 2000).

287 When necessary, variables were log, square-root, arc-sin or box-cox transformed to
288 achieve normality and linearity assumptions. In simultaneous inference for multiple
289 tests, and in order to avoid type I errors, we applied Rice’s sequential correction. We
290 performed an ANOSIM analysis using PRIMER 6.0 (PRIMER-E Ltd, Plymouth, UK)
291 and PC-ORD 4.0 (Version 4, MjM, Gleneden Beach, Oregon MjM) softwares,
292 respectively. We used the R Community Ecology Package “vegan” (Version 1.6-10.
293 <http://cc.oulu.fi/~jarioksa/>) for NMDS, DCA, CCA and pCCA analyses and
294 STATISTICA (Data analysis software system 6, Statsoft 2001, Tulsa, Oklahoma, USA)
295 for Pearson’s product moment correlations and the PCA. We performed Path Analyses
296 with AMOS 5.0 (Version 7.0; SPSS, Chicago).

297

298 **Results**

299 *Floristic and environmental characterization of zones*

300 Along the transect we found a total number of 395 plant species; 56 (14.47%) were
301 woody, 123 (31.13%) perennial and 215 (54.43%) annual herbaceous species,
302 respectively. In general terms the five zones differed in species composition
303 (ANOSIM's $R = 0.5158$, $P < 0.001$). We found the biggest differences were between
304 Aflou and Miliana (ANOSIM's $R = 0.91$, $P < 0.001$) and between Aflou and Blida
305 (ANOSIM's $R = 0.76$, $P < 0.001$) (Appendix A). One-way ANOVA tests revealed
306 overall significant differences between the five zones in perennial herbaceous and
307 woody plant richness, and in climate (mean annual precipitation, mean minimum
308 temperature of the coldest month and quotient of monthly precipitation), soil fertility
309 (percent total and active limestone, pH), soil texture (proportions of sand, silt, fine- and
310 coarse-grained sand, kaollinite, illite and chlorite), and total plant cover (Appendix B).
311 According to Tukey's *post-hoc* tests, the plots in Miliana and Blida were significantly
312 different from those in Aflou, Berrouaghia and Theniet-el-Had in terms of woody plant
313 richness, mean annual precipitation, pH, and proportions of sand, silt and illite. The
314 Aflou plots differed significantly from those in Blida with regard to elevation,
315 **percentage of total** and active limestone, proportions of fine- and coarse-grained sand,
316 and from the plots in Miliana in relation to their values of total plant cover (Appendix
317 B).

318

319 ***Gradients of species composition***

320 The best two-dimensional solution of the NMDS ordination presented a stress value
321 of 0.26 and showed a sharp differentiation of the five zones along the first dimension
322 (Fig. 3). Changes in species composition along the first NMDS dimension were
323 explained by variations in mean minimum temperature of the coldest month and mean
324 annual precipitation, proportion of sand, total plant cover and soil water content (Pf3),

325 in decreasing order of importance. Changes in species composition along the second
326 NMDS dimension were explained by variation in effective cationic exchange capacity.
327 A large amount of variance remains unexplained by environmental or spatial factors
328 (Table 3). Spatial factors (CCA2) explained a higher proportion of variance than
329 environmental factors (CCA1); However, the proportion of variance explained by
330 environmental factors (CCA1) was slightly higher than the proportion of variance
331 explained by the environmental component of spatial influence (pCCA1) (Table 3).

332

333 *Determinants of plant diversity*

334 For the path analysis considering total plant richness as the focus variable, Model E
335 was the best fit for the observed data (Table 4). It revealed a low total unexplained
336 variance ($U = 0.14$) and a positive, strong and significant direct effect of mean annual
337 precipitation on total plant richness (Fig. 4). For path analyses considering woody,
338 perennial herbaceous and annual herbaceous plant richness as the focus variables,
339 Models E, C and E were the best fits of the observed data, respectively (Table 4). They
340 all exhibited low total unexplained variances ($U = 0.35, 0.21$ and 0.12 , Fig. 5). We
341 determined (i) a positive, strong and significant direct effect of mean minimum
342 temperature of the coldest month on woody plant richness (Fig. 5a); (ii) positive and
343 significant direct effects of similar strength of mean annual precipitation and proportion
344 of sand upon perennial herbaceous plant richness (Fig. 5b); and (iii) a significant direct
345 effect of similar strength of mean minimum temperature of the coldest month (negative)
346 and total plant cover (positive) on annual herbaceous plant richness (Fig. 5c).

347 For the path analysis considering species composition as the focus variable, Model
348 D was the best fit of the observed data (Table 4). It revealed a high unexplained
349 variance ($U = 0.74$), and positive, strong and significant effects of mean annual

350 precipitation, total plant cover, and particularly mean minimum temperature of the
351 coldest month, on species composition (Fig. 6).

352 All selected path analyses models showed positive, strong and significant direct
353 effects of mean annual precipitation on soil water content (Pf3) and of proportion of
354 sand on effective cationic exchange capacity, and negative, strong and significant direct
355 effects of soil water content (Pf3) on effective cationic exchange capacity (Figs. 4, 5 and
356 6). None of the models showed any significant direct effect of proportion of sand,
357 effective cationic exchange capacity or soil water content (Pf3) upon total plant cover
358 (Figs. 4, 5 and 6).

359

360 **Discussion**

361 ***Total plant richness and species composition***

362 Changes in total species richness and species composition of *Q. ilex* woodlands
363 along the transect considered in this study were primarily determined by climatic factors
364 related to the precipitation and temperature regimes, namely mean annual precipitation
365 and mean minimum temperature of the coldest month, respectively, a fact which
366 corroborates our initial hypothesis. However, changes in species composition were
367 determined not only by these two climatic factors, but also by total plant cover, and the
368 solved path diagram for determinants of this focus variable showed stronger
369 relationships than those of the solved path diagram for determinants of total plant
370 richness. This suggests that species composition, which is more related to beta and
371 taxonomic diversity, reflects processes regulating species coexistence and segregation in
372 space much better than total species richness, which is more closely related to alpha
373 diversity (Purvis and Hector, 2000; Balvanera et al. 2002). However, the high
374 unexplained variance of the solved path diagram for determinants of species

375 composition indicates that other factors different from those considered in this study
376 may be affecting changes in variables across the transect considered. This result can be
377 explained by the existence of some differences in the dominant bedrock types in the five
378 zones selected along the study area. In these zones most of the plots are located over
379 limestone, sandstone, schists, quartzites, loam and clay substrates, but the proportion of
380 those located over limestone substrates is higher in Aflou (Ihaddaden, pers.
381 observation). Spatial locations (namely elevation and latitude) influenced species
382 composition of plots. However, the species variation explained by environmental
383 factors showed a slight decrease (from 13.96 to 13.38%) when the effects of spatial data
384 were statistically controlled. The potentially confounded effects of spatial locations and
385 environmental factors on species composition are therefore low.

386

387 *Species richness of life-forms*

388 Likewise, as we hypothesized, changes in woody plant richness were primarily
389 determined by factors related to the temperature regime. The effect of mean minimum
390 temperature of the coldest month on woody plant richness was strong and positive,
391 which is related to the high woody plant richness seen in the warmest zones of the study
392 area (Blida and Miliana). This may be explained by the low tolerance of many woody
393 plants (particularly trees) to extreme cold temperatures in the Mediterranean climate
394 zones of the world due to limitations to photosynthesis and plant growth (Larcher
395 2000). Nonetheless, mean minimum temperature of the coldest month was also the most
396 important factor explaining changes in species composition. These results fit with the
397 predictions of Dahmani-Megrerouche (2002) for *Quercus ilex* woodlands in Northern
398 Algeria and complement recent findings in the mountains of Northern Morocco, which
399 emphasize that changes in species composition along altitudinal gradients are chiefly

400 determined by the differential tolerance of woody plants to cold conditions (Ajbilou et
401 al., 2006). Similarly, our results suggest that changes in species composition along the
402 latitudinal transect considered are closely associated with changes in woody plant
403 richness. Moreover, Miliana and Blida, the zones showing the highest total and woody
404 plant richness values, also receive the greatest amount of rain along the transect studied,
405 which implies that the effects of mean minimum temperature of the coldest month on
406 species composition are greater where mean annual precipitation is higher (Kadmon and
407 Danin 1999). The strong, positive and significant indirect effect of mean annual
408 precipitation on woody plant richness through soil water content (Pf3) provides support
409 for this hypothesis. It is interesting to note, however, that the direct effect of soil water
410 content (Pf3) on woody plant richness is weak, negative and non-significant, a fact that
411 might be explained by the relative tolerance of many woody species to semi-arid
412 conditions (Bonet and Pausas 2004).

413 Changes in perennial herbaceous plant richness were mainly determined by factors
414 associated with the precipitation regime (mean annual precipitation), but not by soil
415 water content (Pf3). Both perennial and annual herbaceous plants use the transient water
416 stored in the topsoil (Lu et al., 2006). Nonetheless, under conditions of high soil water
417 availability, perennials are more competitive than annuals because they have greater
418 root plasticity and resistance to hydraulic flows in roots, which enable them to make
419 more rapid use of the transient water synchronic with precipitation pulses such as
420 infrequent summer rains (De Lillis et al., 2005). Along the transect considered, the
421 highest values for perennial herbaceous plant richness were observed in Miliana and
422 Blida, the zones with the highest mean annual precipitation, and where summer drought
423 is the shortest and least intense. This has been observed over broad-scale transition
424 biomes such as the arid and semi-arid grasslands of North America (Hochstrasser et al.,

425 2002) and the Iberian Peninsula (Clary, 2008) and agrees with the predictions by Floret
426 et al. (1990) for Northern Algeria. The strong, positive and significant effect of the
427 proportion of sand on perennial herbaceous plant richness may be explained by the
428 more regular and higher primary productivity of sandy areas than that of finer-textured
429 soils in Northern Africa (Le Houérou 2001). This effect might also be related with the
430 strong relationship between mean annual precipitation and perennial herbaceous plant
431 richness, as there is more rapid weathering of fine-grained soil particles (i.e. silt and
432 clay) in soils in zones receiving the highest amount of precipitation and in turn, the
433 proportion of sand therein tends to be high (A. Ihaddaden, personal observation).

434 In contrast to our hypothesis, changes in annual herbaceous plant richness were
435 were primarily affected by mean minimum temperature of the coldest month and total
436 plant cover. Interestingly, the effect of mean minimum temperature of the coldest month
437 on annual herbaceous plant richness was strong but negative, which could be related to
438 the high level of annual herbaceous plant richness in the coldest zones of the transect
439 (i.e. Aflou, Berrouaghia and Theniet-el-Had). Moreover, the strong negative and
440 positive effects of mean minimum temperature of the coldest month on annual
441 herbaceous and woody plant richness, respectively, might be related to the differential
442 tolerance of these life-forms to cold conditions (Bhattarai and Vetaas 2003), and this
443 fact might influence changes in species composition along the transect studied.
444 Furthermore, we found strong, positive and significant effects of total plant cover on
445 annual herbaceous plant richness and species composition, and the most arid (i.e. Aflou)
446 and mesic (i.e. Blida) of our study zones comprised one of the highest and lowest
447 annual herbaceous plant richness, respectively. These results suggest a change in the
448 relative dominance of facilitation and competition between woody and annual
449 herbaceous plants from south to north along the studied transect. This agrees with the

450 *stress gradient hypothesis*, which predicts that negative (i.e. intra- and inter-specific
451 competition) and positive (i.e. facilitation) interactions often prevail in the mildest and
452 the harshest zones of environmental gradients, respectively (Bertness and Callaway,
453 1994). Similar results have been obtained in studies conducted at local (Holzapfel et al.,
454 2006) and regional (Armas et al., 2011) scales in the Mediterranean basin. It should also
455 be noted that in Blida, five plots were sampled in 1991 and ten in 1999, and mean
456 annual precipitation in these two years was slightly higher than in 1990 (*Office National*
457 *de la Météorologie*, Algiers). The amount and rhythm of precipitation influences seed
458 production, germination and the establishment of annual plants in the semi-arid
459 Mediterranean (Sher et al., 2004). Therefore, the higher mean annual precipitation in
460 1991 and 1999 compared to 1990 could have increased the richness of annual
461 herbaceous plants in Blida, thus biasing our results. However, Blida presents the mildest
462 climate in the transect considered (accounting for the highest mean annual rainfall and
463 the least quotient of monthly precipitation), and presented the lowest richness of annual
464 species. Thus, it is unlikely that differences in the total amount and intra-annual
465 variations of precipitation between 1990/1991 and 1999 could have strongly affected
466 annual herbaceous plant richness in the plots in this zone.

467

468 ***Soil conditions and total plant cover***

469 Proportion of sand and soil water content (Pf3) did not show any direct and
470 significant effect on total plant cover, but indirectly affected this variable through their
471 effects on the capacity for effective cationic exchange. These results point towards the
472 important role played by total plant cover as a mediator of the effects of soil conditions
473 on plant diversity (Ehrenfeld et al., 2005). This contrasts with the results of García-
474 Fayos and Bochet (2009) who found that, in Mediterranean shrublands, plant species

475 richness was mainly and directly correlated with soil conditions, which implies that, in
476 the *Q. ilex* woodlands considered in this study, total plant cover has not been depleted
477 beyond irreversible thresholds, a fact that would lead to desertification (e.g. Moreno de
478 las Heras et al., 2009). Thus, total plant cover is strongly and positively related to plant
479 diversity and may be considered a good indicator of ecosystem health (Torras et al.,
480 2008).

481

482 ***Human use***

483 It is also important to point out that, although the history of the effects of human
484 uses was not considered at the plot scale and not considered in the analyses, this history
485 could be important with regard to explaining the high annual plant richness in Aflou,
486 Berrouaghia and Theniet-el-Had. The high annual herbaceous plant richness in Aflou
487 could be explained by the fact that this zone, which presents a semi-arid climate, bears a
488 high livestock load (Table 2), and establishment and germination of annual herbaceous
489 plants are usually favoured by grazing in semi-arid areas (De Bello et al., 2005). In
490 Berrouaghia and Theniet-el-Had, the high richness of annual herbaceous plants may be
491 explained by the fact that these two areas, which present a mesic climate, also harbour a
492 large human (and mainly rural) population, and their *Q. ilex* woodlands suffer from
493 intense fuel extraction for domestic use (A. Ihaddaden, personal observation). In areas
494 of intermediate seasonality, annual herbaceous plants tend to fill open spaces, acting as
495 r-selected ruderals (Clary 2008). Thus, in these two zones, they could have invaded the
496 areas degraded by intense human use. The presence in Berrouaghia and Theniet-el-Had
497 of species such as *Stipa tenacissima* and *Ampelodesmos mauritanica*, which are often
498 associated with landscape degradation as a result of human-induced disturbance (Le
499 Houérou, 2001; Maestre, 2004), provides additional support for this hypothesis.

500 Moreover, along the studied transect, the percentage of annual herbaceous plants
501 (54.43%) was much higher than the percentages of perennial herbaceous (31.13%) and
502 woody (14.47%) plants among the total number of species. This contrasts with findings
503 of Dahmani-Megrerouche (1996), who reported less contrasting percentages for these
504 life forms in Algerian *Q. ilex* woodlands. Therefore, our findings highlight more intense
505 landscape degradation than expected in the study area.

506

507 ***Implications***

508 Our results provide support for some of the hypotheses put forward in the introduction.
509 They indicate that changes in plant diversity of *Q. ilex* woodlands in Northern Algeria
510 are mainly influenced by environmental factors related to the precipitation and
511 temperature regimes, and by total plant cover. Climate change predictions for the
512 southern boundary of the Mediterranean basin suggest an increase in mean annual
513 temperature and a reduction of soil water content (Gao and Giorgi, 2008). This, together
514 with the reduction of total plant cover derived from human activities (Vogiatzakis et al.,
515 2006, Underwood et al., 2009), may have profound consequences for the vegetation
516 studied, such as a decrease in total plant richness and that of perennial herbaceous
517 plants, chiefly in the humid and sub-humid zones of the Northern side of the Tell Atlas.
518 Sustainable management of remnant *Q. ilex* woodlands in Northern Africa is needed to
519 avoid degradation of the vegetation cover and to maintain plant diversity, functional
520 status and provision of ecosystem services. It should be pointed out that, although our
521 approach enables us to elucidate the main environmental factors determining changes in
522 plant richness across the studied transect, it is unable to elucidate the underlying
523 processes, which must be subjected to experimental verification (Petraitis et al., 1996).

524

525

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537

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671

TABLES

Table 1 Climatic conditions of the five zones considered in the present study (Aflou, Berrouaghia, Theniet-el-Had, Miliana and Blida), according to records from the nearest meteorological stations. Data were provided by the *Office National de la Météorologie* (Algiers).

Zone	Aflou	Berrouaghia	Theniet-el-Had			Miliana		Blida		
Meteorological station	Aflou	Berrouaghia	Bir Ghbalou	Theniet- el-Had	Bord el emir Abdelkader	Miliana	Blida	Lac Mouzaia	Camp des Chênes	Chr�ea
Latitude	34°7'N	36°8'N	36°16'N	35°52'N	35°52'N	36°19'N	36°28'N	36°22'N	36°22'N	36°2'N
Longitude	2°6'E	2°55'E	3°35'E	2°1'E	2°16'E	2°14'E	2°50'E	2°41'E	2°47'E	2°53'E
Elevation (m a.s.l.)	1406	925	642	1160	1050	750	267	1270	941	1550
Time of measurement (years)	1965-95	1965-95	1968-95	1968-95	1972-95	1960-95	1960-95	1960-95	1970-1995	1960-1995
Number of plots	15	18	7 ^a	11 ^a	4 ^a	9	2 ^b	17 ^b	12 ^b	9 ^b
Mean annual precipitation (MAP) (mm)	340	593	542	620	520	950	950	930	990	1380
Quotient of monthly precipitation; monthly SD / monthly mean precipitation (mm)	0.355	0.608	0.555	0.537	0.540	0.715	0.543	0.680	0.829	0.647
Mean summer rainfall (mm)	48	24	35	38	47	36	47	37	18	70
Mean annual number of days of precipitation	66	60	59	72	81	98	NA	88	NA	NA
Mean annual temperature (MAT) (�C)	13.1	14.2	NA	13.5	NA	15.7	18.3	11.7	NA	11
Mean of the minimums of the coldest month (�C)	-1,3	0,6	NA	0,2	NA	4,6	7.3	1.0	NA	0,4

Mean of the maximums of the warmest months (°C)	33.0	34.2	NA	32	NA	31.1	33.6	28.8	NA	26.3
Evapotranspiration (m/year)¹	0.29	0.47	NA	0.48	NA	0.65	0.68	0.57	NA	0.56

^a In Theniet-el-Had we used precipitation data from the Bir-Ghbalou and Bord el emir Abdelkader meteorological stations for 7 and 4 plots, respectively, and temperature data from the Theniet-el-Had meteorological station for all 11 plots.

^b In Blida, we used precipitation data from the Champ des Chênes meteorological station and temperature data from the Lac Mouzaia meteorological station for 12 plots.

¹ We calculated evapotranspiration with the Coutagne method (Remenieras 1974): $ET = MAP - \lambda MAP^2$, where $\lambda = 1 / (0.8 - 0.14 * MAT)$. MAP = Mean annual precipitation, MAT = Mean annual temperature.

1 **Table 2** Area and surrogates of human-use intensity of the five zones considered in the
 2 study (Aflou, Berrouaghia, Theniet-el-Had, Miliana and Blida). Data on human
 3 population density and density of cows, sheep and goats (numbers / km²) correspond to
 4 the different provinces (Wilayas) in which the five study zones are located, and were
 5 obtained from the *Office National des Statistiques* (Algiers). Number of cows and
 6 number of sheep and goats are referred to as cattle and livestock load, respectively.

7
 8

Zone	Aflou	Berrouaghia	Theniet-el-Had	Miliana	Blida
Province (Wilaya)	Laghouat	Médeâ	Tissemssilt	Ain Defla	Blida
Area of <i>Quercus ilex</i> woodlands (ha)	1,350	6,900	1,545	1,860	10,500
Human population density (number / km²)	6.89	83.66	40.47	108.26	298.04
Density of cows (number / km²)	0.80	5.06	4.69	7.13	11.94
Number of sheep (number / km²)	52.17	71.74	52.34	36.74	25.95
Number of goats (number / km²)	9.61	5.48	1.47	5.07	5.62

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Table 3 Summary of results of ordination analyses performed for variance partitioning, including: unconstrained (DCA), constrained by environmental factors (CCA1) and spatial data (CCA2), constrained by environmental factors after adjusting by the best predictors among spatial data (pCCA3), and constrained by spatial data after adjusting with the best predictors among the environmental factors (pCCA4). For each analysis, the sum of all eigenvalues (trace), the percentage of variance explained, the degrees of freedom, the F value and the statistical significance of the model (assessed by 999 Monte Carlo permutations) are shown.

Analysis	Constrained by	Covariables	Trace	% Variance explained	df	F
DCA	-	-	1.0328	100	8	-
CCA1	Environmental factors	-	0.8958	13.96	8	1.48**
CCA2	Spatial data	-	0.9595	15.02	3	2.12**
pCCA3	Environmental factors	ELE, LAT	0.6649	13.38	8	1.29**
pCCA4	Spatial factors	MAP, MTC	0.7047	14.47	3	1.58**

Table 4 Summary of results of the Path Analysis for determinants of total species richness, woody, perennial and annual herbaceous plant richness and species composition in *Quercus ilex* woodlands in northern Algeria. Model A is the *a-prioristic* model proposed in Fig. 2. Models B, C, D, E, F and G have one, two, three, four, five and six removed paths, respectively. Values of χ^2 (with degrees of freedom and *P*), NFI and GFI statistics from “Chi-square”, Bentler and Bonett’s normed-fit and the Goodness-of-fit tests are shown. Boldface indicates the models finally selected.

Focus	Model	X ²	d.f.	P	GFI	NFI	RMSEA
Total species richness¹	Model A	4.70	2	0.095	0.984	0.965	0.130
	Model B	4.81	3	0.186	0.984	0.964	0.087
	Model C	4.81	4	0.307	0.984	0.964	0.051
	Model D	4.82	5	0.438	0.984	0.964	0.000
	Model E	4.89	6	0.557	0.983	0.964	0.000
	Model F	5.727	7	0.572	0.980	0.957	0.000
Woody plant richness²	Model A	4.70	2	0.095	0.984	0.970	0.130
	Model B	4.70	3	0.195	0.984	0.970	0.084
	Model C	4.71	4	0.318	0.984	0.970	0.047
	Model D	4.72	5	0.451	0.984	0.970	0.000
	Model E	4.812	6	0.568	0.983	0.969	0.000
	Model F	5.400	7	0.611	0.981	0.966	0.000
	Model G	6.385	8	0.604	0.978	0.959	0.000
Perennial herbaceous plant richness³	Model A	4.703	2	0.095	0.984	0.967	0.130
	Model B	4.704	3	0.195	0.984	0.967	0.084
	Model C	4.710	4	0.318	0.984	0.967	0.047
	Model D	4.733	5	0.449	0.984	0.967	0.000
	Model E	5.563	6	0.474	0.981	0.961	0.000
Annual herbaceous plant richness⁴	Model A	4.691	2	0.096	0.984	0.965	0.130
	Model B	4.694	3	0.196	0.984	0.965	0.084
	Model C	4.705	4	0.319	0.984	0.965	0.047
	Model D	4.888	5	0.430	0.983	0.963	0.000

	Model E	5.026	6	0.540	0.983	0.962	0.000
	Model F	5.856	7	0.557	0.980	0.956	0.000
Species composition⁵	Model A	4.703	2	0.095	0.984	0.980	0.130
	Model B	4.704	3	0.195	0.984	0.980	0.084
	Model C	4.710	4	0.318	0.984	0.980	0.047
	Model D	4.792	5	0.442	0.984	0.979	0.000
	Model E	5.137	6	0.526	0.983	0.978	0.000
	Model F	7.501	7	0.379	0.975	0.968	0.030

^{1, 2, 3, 4} Model A: all relationships (Fig.2)

¹ Model B: without 2; Model C: without 2 and 14; Model D: without 2, 14 and 15; Model E: without 2, 14, 15 and 4.

² Model B: without 15; Model C: without 15 and 14; Model D: without 14, 15 and 6; Model E: 15, 14, 6 and 3; Model D: without 15, 14, 6, 3 and 5; Model E: without 15, 14, 6, 3, 5 and 4.

³ Model B: without 15; Model C: without 15 and 14; Model D: 15, 14 and 4; Model E: without 15, 14, 4 and 10.

⁴ Model B: without 14; Model C: without 14 and 15; Model D: without 14, 15 and 6; Model E: without 14, 15, 6 and 1; Model F: without 14, 15, 6, 1 and 10.

⁵ Model B: without 15; Model C: without 15 and 14; Model D: without 15, 14 and 5; Model E: without 15, 14, 5 and 6; Model F: without 15, 14, 5, 6 and 4.

Figures

Fig. 1. (a) Location of the study area showing the potential distribution area of *Quercus ilex* sp. *rotundifolia* (in grey). (b) Detailed map of the aridity gradient considered in the study showing isohyets of mean annual precipitation (mm) (in black), areas occupied by *Q. ilex* sp. *rotundifolia* woodlands (in grey), and locations of the five sampling zones selected, namely Blida and Miliana (sub-humid/warm), Berrouaghia (sub-humid/cold), Theniet-el-Had (dry/cold) and Aflou (very dry/cold).

Fig. 2. Path diagrams of the *a-prioristic* initial model (Model A) hypothesizing the relationships among each of the focus variables (total species richness, woody, perennial and annual herbaceous plant richness, or species composition), and mean annual precipitation (MAP), mean minimum temperature of the coldest month (MTC), total plant cover (TVC), proportion of sand, soil water content (Pf3) and effective cationic exchange capacity. Relationships, residual correlations and unexplained variances of exogenous variables are depicted by single-headed arrows, double-headed arrows, and arrows not originating at any variable (U), respectively. Numbers match the relationships explained in the main text. According to this model, all focus variables are primarily determined by MAP, MTC, TVC, soil water content (Pf3), effective cationic exchange capacity and proportion of sand (paths 1 to 6). TVC is, in turn, determined by MAP, MTC, proportion of sand, soil water content (Pf3) and effective cationic exchange capacity (paths 7 to 11). Soil water content is determined by MAP, MTC and proportion of sand (paths 12 to 14), and effective cationic exchange capacity is determined by MAP, soil water content and proportion of sand (paths 15 to 17). Residual correlations between MAP, MTC and proportion of sand are represented by paths 18 to 20.

Fig. 3. Non-metric Multidimensional Scaling ordination of species composition in the 81 plots considered in the study, showing the interpretation of the ordination axes with respect to

major environmental factors. Species composition is expressed as coordinates of the sample plots. Symbols (both, full and empty) indicate plots, crosses indicate species and arrows indicate environmental factors. The smoothing surface lines (Oksanen et al., 2010) for mean annual precipitation are shown in grey.

Fig. 4. Solved path diagram for determinants of total species richness (Model E in Table 4). Single-headed arrows depict directional relationships, whereas two-headed arrows depict correlations. Arrows in bold indicate strong and significant relationships. Numbers indicate standardized path coefficients and asterisks denote path coefficients that are significantly different from zero as assessed by multivariate Wald tests.

Fig. 5. Solved path diagram for determinants of woody plant richness (a), perennial herbaceous plant richness (b) and annual herbaceous plant richness (c) (Models E, C and E, respectively, Table 4). Single-headed arrows depict relationships, whilst two-headed arrows depict correlations. Arrows in bold indicate strong and significant relationships. Numbers near the paths indicate standardized path coefficients and asterisks denote path coefficients that are significantly different from zero as assessed by multivariate Wald tests.

Fig. 6. Solved path diagram for determinants of species composition (Model E in Table 4). Single-headed arrows depict direct relationships, whereas two-headed arrows depict correlations. Arrows in bold indicate strong and significant relationships. Numbers indicate standardized path coefficients and asterisks denote path coefficients that are significantly different from zero as assessed by multivariate Wald tests.

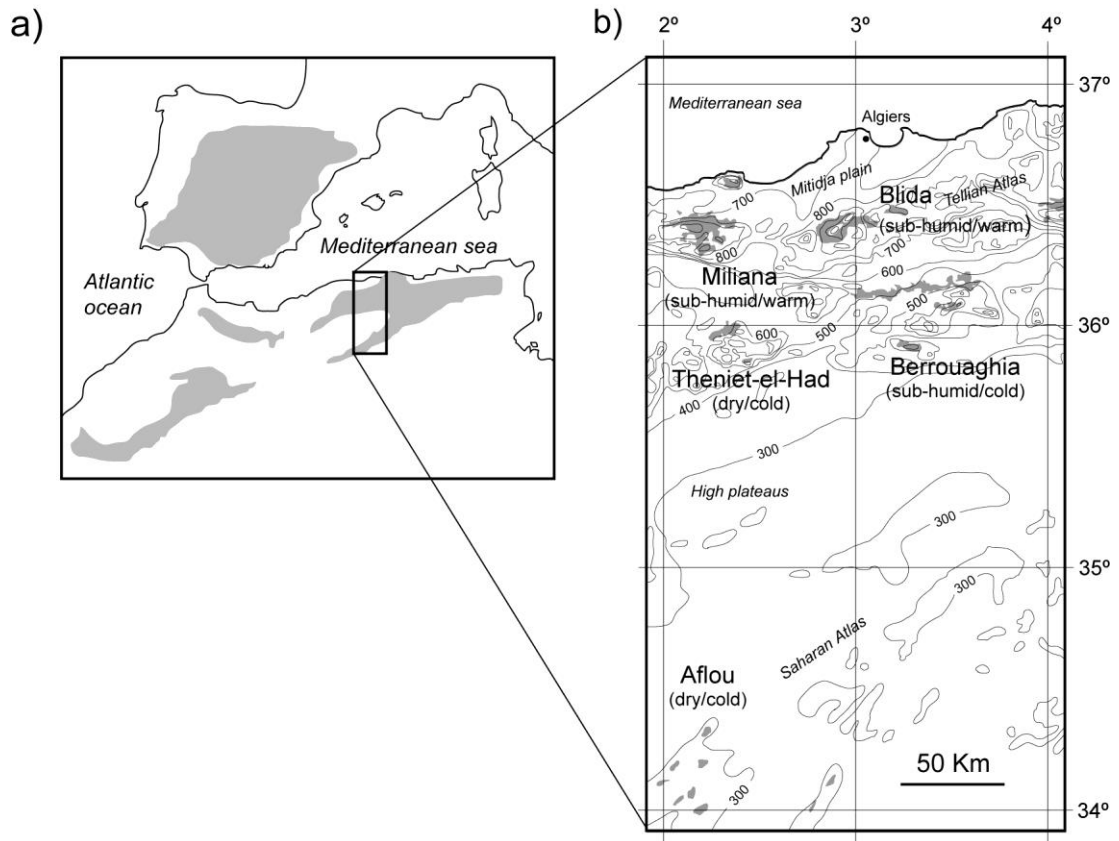


Figure 1

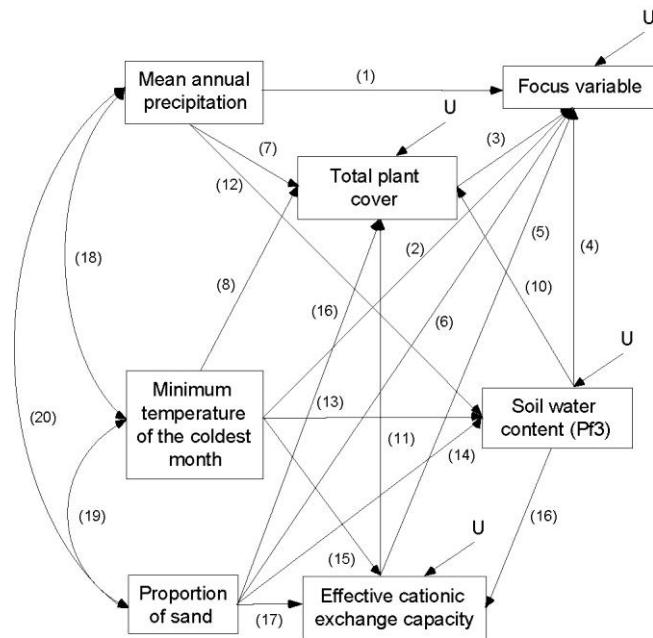


Figure 2

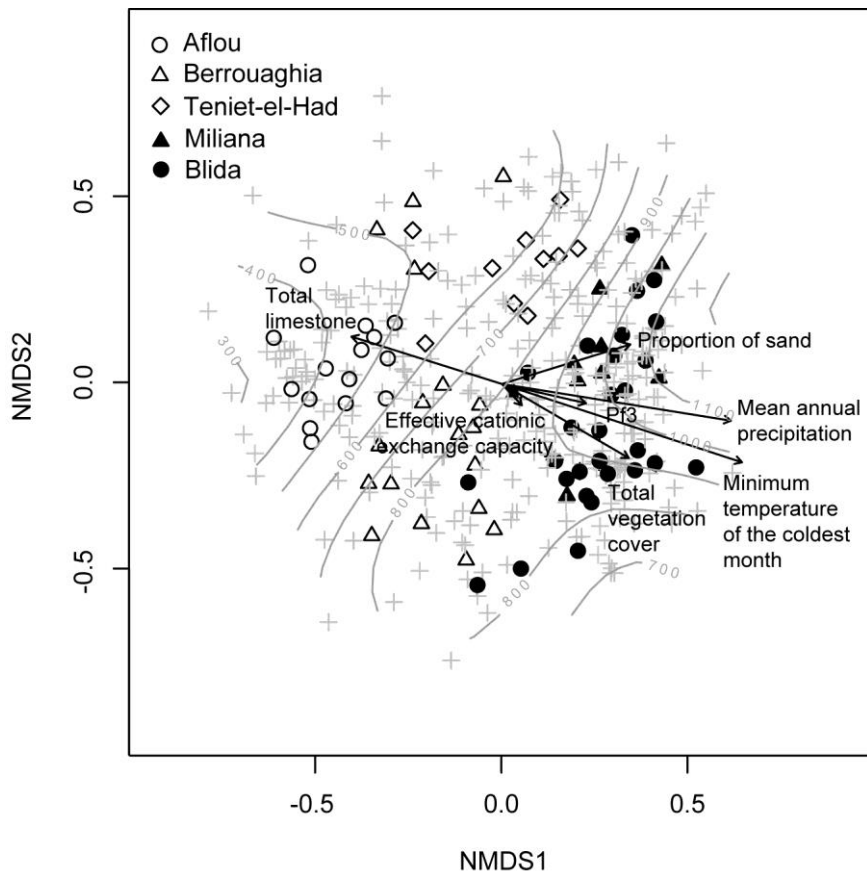


Figure 3

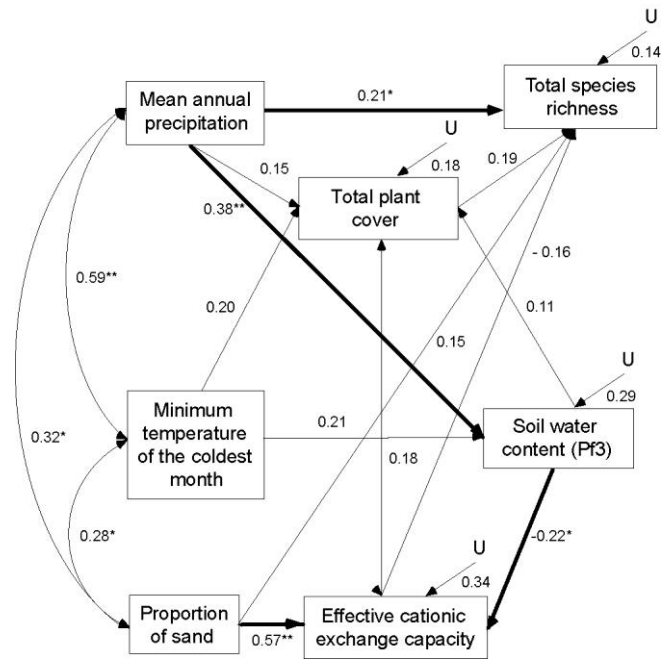


Figure 4

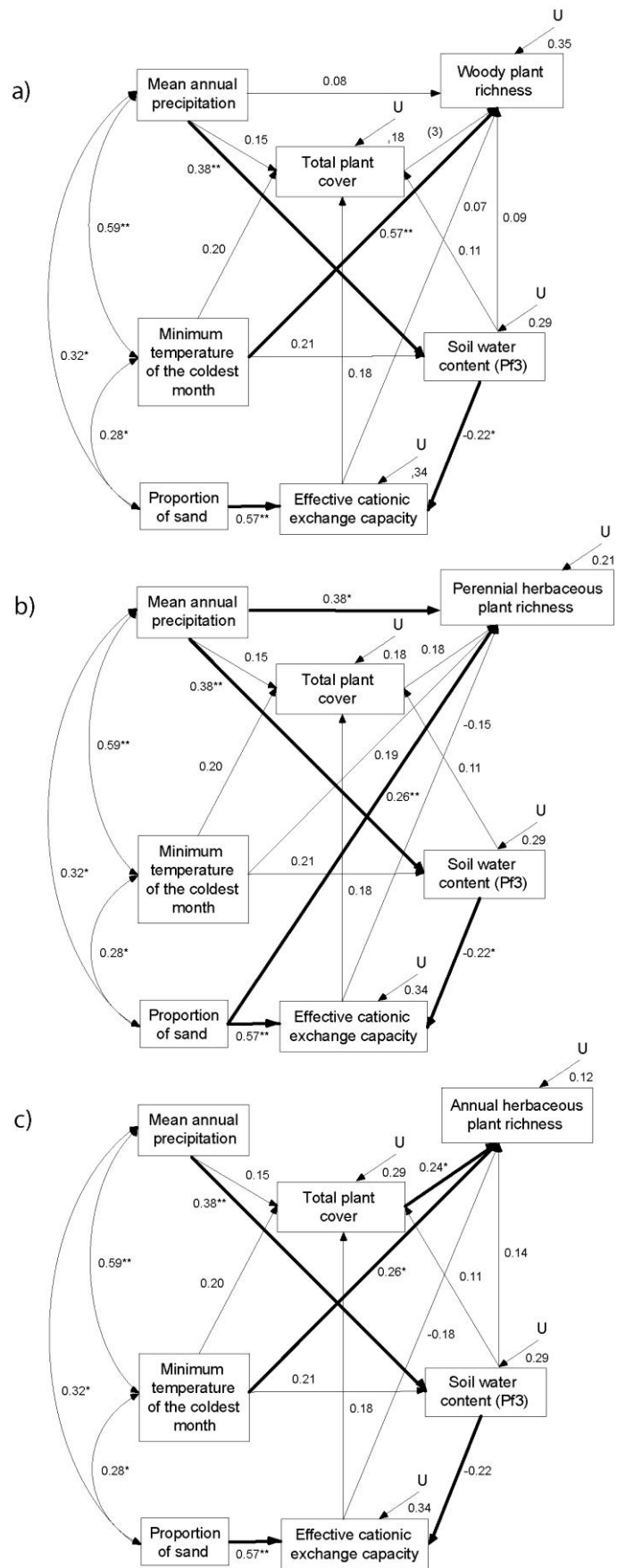


Figure 5

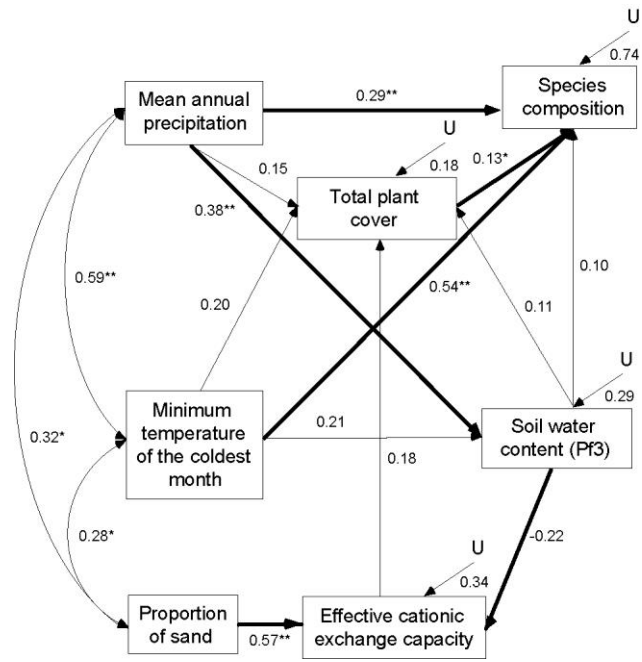


Figure 6