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1 **The state of change of *Erica scoparia* L. heathland through cattle grazing and oak**
2 **colonisation**

3

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16

17 **SUMMARY**

18 Our aim was to ascertain whether changes in plant species richness and other vegetation
19 features occur in heath land dominated by *Erica scoparia* L. (besom heath) through the
20 impact of cattle grazing and oak colonisation. Our study took place in the Brenne
21 Regional Natural Park (center of France) where this ericaceous species, locally called
22 ‘brande’, is now considered of patrimonial interest and protected at regional and
23 European level. We selected 10 sites in a private property, covering a wide range of
24 ecological conditions (shallow and deep soils, grazed and non-grazed besom heath, pure
25 and oak-colonised besom heath). Vegetation (percent occupancy of plant species) was
26 sampled in May-June 2006 (105 samples, 1m² each) and the impact of shrub and tree
27 vegetation on plant biodiversity was assessed by correspondence analysis (CA) and total
28 and partial Mantel tests (Monte-Carlo procedure). An environmental gradient of
29 decreasing light incidence from grazed heath to old heath to oak-wood was depicted,
30 along which a number of ecological, morphological and physiological plant traits
31 (growth habits, Ellenberg values, Grime strategies, Tolerance Index of the plant
32 community) were observed to vary. Species richness decreases when ericaceous or,
33 although to a lesser extent, oak cover increase and it increases under low to moderate
34 cattle grazing. Consequences for the sustainable management of ‘brande’ are discussed.

35

36 Keywords: ericaceous heath, plant traits, plant biodiversity, Ellenberg values, Grime
37 strategies, Tolerance Index

38

39 **RÉSUMÉ**

40 Le but de notre étude est de mettre en évidence les modifications de la richesse
41 spécifique et d’autres caractères de la végétation qui surviennent sous l’influence du

42 pâturage et de la colonisation par le chêne dans les landes dominées par *Erica scoparia*
43 L. (brande). L'étude a été menée dans le Parc Naturel Régional de la Brenne (France,
44 Région Centre) où cette Éricacée est aujourd'hui considérée comme patrimoniale et
45 protégée au niveau régional et européen. Dix sites ont été choisis au sein d'une propriété
46 privée, couvrant un large éventail de conditions écologiques (sols superficiels et
47 profonds, brande pâturée et non pâturée, pure et envahie par le chêne). La végétation
48 (pourcentage d'occupation de l'espace par les différentes espèces végétales) a été
49 échantillonnée en mai et juin 2006 (105 relevés d'1 m²) et l'impact de la végétation
50 arbustive et arborée sur la biodiversité végétale a été mis en évidence à l'aide de
51 l'analyse des correspondances (AFC) et de tests de Mantel totaux et partiels (méthode
52 de Monte-Carlo). Un gradient décroissant d'incidence de la lumière a été mis en
53 évidence depuis la brande pâturée jusqu'à la brande âgée puis la chênaie, en rapport
54 avec la variation de nombreux traits écologiques, morphologiques et physiologiques
55 (types physiologiques, indices d'Ellenberg, stratégies de Grime, indice de tolérance de
56 la communauté). La richesse spécifique décroît à mesure de l'extension des Éricacées
57 ou, dans une moindre mesure, de celle du chêne et s'accroît sous pâturage faible à
58 modéré. Les conséquences pour la gestion durable de la brande sont discutées.

59

60 Mots-clés: lande à Éricacées, traits végétaux, biodiversité végétale, indices d'Ellenberg,
61 stratégies de Grime, indice de tolérance

62

63 **Introduction**

64

65 *Erica scoparia* L. (besom heath) is a tall shrub species which dominates mesic
66 heathlands of South-western France and North-western Spain (Bartolomé *et al.*, 2005).

67 On poorly fertile soils, it establishes spontaneously by seed in grassland after
68 agricultural abandonment and before oak colonisation (Perrinet, 1995). Once
69 established, this tall ericaceous shrub (2-3m height) grows vegetatively and resprouts
70 after cutting. It forms dense clumps in the shade of which a 'forest' environment is
71 created. Given the poor pastoral value of ericaceous heath and its richness in
72 allelochemicals (Ballester *et al.*, 1982), fire was used to suppress it at least temporarily
73 for the sake of sheep or cattle grazing (Gimingham *et al.*, 1979; Bartolomé *et al.*, 2005).
74 However, *E. scoparia* was also and is still cultivated for traditional purposes (broom,
75 fencing manufacture or roof making), thereby contributing to its widespread occurrence
76 in the temperate Atlantic region, especially on former agricultural land (Perrinet, 1995;
77 Bartolomé *et al.*, 2005).

78

79 In the Brenne Regional Natural Park (Indre, Centre, France), heathland
80 dominated by *E. scoparia*, locally called 'brande' (the name indicate both the plant and
81 the community), covers wide areas of land not managed for agriculture (Rallet, 1935). It
82 is now protected, according to European policies for the conservation of heathland
83 habitats (European Council Directive 92/43). However, the conservation value of
84 'brande' imposes to preserve it from spontaneous colonisation by several oak species
85 [*Quercus robur* L., *Q. petraea* (Matt.) Liebl., *Q. pubescens* Willd. and their hybrids]
86 could occur. Cutting, moderate grazing or prescribed burning are used for the
87 management of *E. scoparia* heathland, which is considered of a higher patrimonial
88 interest, when at an early successional stage, than the succeeding old heath and oak-
89 wood stages (Gaudillat, 1997). In the particular landscape of 'Grande Brenne' (60,000
90 ha, included in the Brenne Natural Park) hard sandstone outcrops of poor agricultural
91 value, locally called 'buttons', are often covered with a dry variant of *E. scoparia* heath,

92 with common heather (*Calluna vulgaris* L.) and bell heather (*Erica cinerea* L.) as
93 companion species (Rallet, 1935). Colonization by oak is more difficult on ‘buttons’,
94 due to shallow soil conditions, and some of these outcrops appear devoid of any shrub
95 vegetation, with an abundant and diversified herb, moss and lichen vegetation
96 (Gaudillat, 1997). ‘Buttons’ are surrounded by more mesic environments, most often
97 used for pasture, with stagnant water during winter and spring months (Rallet, 1935).
98 Other important components of the Grande Brenne landscape are numerous ponds,
99 traditionally created from the Middle Age for the need of carp breeding.

100

101 Our aim was to ascertain whether changes in plant species richness and other
102 vegetation features occur in *E. scoparia* heath through the impact of cattle grazing and
103 oak colonisation. The negative impact of dense ericaceous heath on plant species
104 richness has been often recorded (Barclay-Estrup & Gimingham, 1969; Gimingham *et*
105 *al.*, 1979; Miles, 1979) and we hypothesized that this detrimental effect could be
106 alleviated under either moderate grazing by cattle or colonisation by oak.

107

108 **Methods**

109

110 Study sites

111

112 The present study was done in a private property (Les Vigneaux, Mézières-en-Brenne,
113 Indre), where the traditional land use of Grande Brenne has been maintained to a large
114 extent, displaying a variety of typical environments: ‘buttons’ with shallow soils are let
115 covered with spontaneous scrub and forest vegetation while the surrounding land
116 (meadows and ponds) is devoted to extensive cattle pasture and to fishing. Such

117 practices have been widely maintained in Grande Brenne for several centuries
118 (Trotignon & Trotignon, 2007). The landscape includes two 'buttons' covered with
119 grazed or non-grazed ericaceous heath and woodlots of natural oak and planted pine and
120 poplar. Ponds and meadows are also present but they were not included in our study.
121 We selected ten sites (Fig. 1) covering the range of variation of non-agricultural land,
122 from grazed heath to oak woodland, thus expressing a gradient of decreasing opening of
123 the environment and increased vertical stratification (Table 1). They were chosen on the
124 base of a previous map of vegetation done by F. Pinet (personal communication) and
125 our own observations on plant communities. Soils were classified as shallow or deep
126 whether they were less or more than 20cm deep. Two intensities of grazing could be
127 ascertained from the morphology of besom heath: in BP1 bushes kept more or less their
128 natural erected form, while in BP2 they exhibited a typical conical shape resulting from
129 the selection of twigs of the year by cattle. BNP did not exhibit any sign of cattle
130 pressure, being located on Button 2, from which cattle was excluded. BA1, BA2 and
131 BA3 were old besom heath sites, hardly accessible and not used by cattle.

132

133 The elevation is around 120m a.s.l., with an undulating relief due to an
134 alternation of 'buttons' and ponds. The climate is Atlantic, mild oceanic, with a mean
135 annual temperature of 11°C and a mean annual rainfall of 700mm. Soils are highly
136 heterogeneous, varying from Lithosols (top of 'Buttons') to Gleysols (pond shores, not
137 studied here). According to data on BP1, BP2 and BA1 (Benoist, 2006) the topsoil of
138 pastured and old heath is acid ($\text{pH}_{\text{water}} \sim 4.5$) and moderately fertile ($\text{C/N} \sim 18$). These
139 features are quite similar to those of woodlots ($\text{pH}_{\text{water}} \sim 4.4$, $\text{C/N} \sim 19$) but differ from
140 those of pastures ($\text{pH}_{\text{water}} \sim 4.9$, $\text{C/N} \sim 14$). The Humus Index (Ponge & Chevalier, 2006)

141 varies to a great extent, from 1 (Eumull) in BP1 to 5.8 (Eumoder) in average in BP2
142 (Benoist, 2006).

143

144 Sampling procedure

145

146 Stratified sampling of vegetation took place in June 2006. The sites CHM1, CHM2,
147 BSF1, BSF2, BA3 and BA2 were sampled as follows: four 1m² squares were disposed
148 at each angle of a 10 x 10m square and an additional 1m² square was placed at the
149 centre. Each unit square was divided into 25 sub-units according to a 20cm grid,
150 allowing to score plant species by counting the number of sub-units where they were
151 found (ranging from 0 to 25) which was an estimate of their occupancy. When trees
152 were present the projection of their crown was used for the calculation of their score.
153 Only four unit squares could be positioned in BA3, one corner being omitted by lack of
154 space. The choice of a small and constant plot size for our stratified sampling was
155 justified by the need to measure plant species richness at a very local level, and to
156 compare it among different ecosystem types.

157

158 BNP was sampled along eight transect lines radiating from a central post. Unit
159 squares were positioned each 4m. The number of unit squares along a given direction
160 varied from 2 to 5, totalling 29 samples.

161

162 BP1, BP2 and BA1 were sampled by positioning unit squares each 6m along
163 several rows placed 7m apart, the total number of samples varying according to the site
164 shape.

165

166 Differences in sampling design were mainly due to topographic variation and the
167 need to embrace most visible intra-site heterogeneity. However, distances between unit
168 squares within each site remained of the same order of magnitude (4 to 7m), and
169 allowed to embrace the whole area covered continuously by a given vegetation type.

170

171 Mosses and vascular plants were identified at the species level whenever
172 possible (Table 2).

173

174 Data analysis

175

176 Species richness was calculated as the number of plant species found in each 1m² unit
177 square (Table 1). We used species richness at the plot scale (a small-scale community
178 attribute) as a measure of species coexistence (a small-scale community process),
179 considering that the more species co-occurring at a very small-scale (1m²), the less
180 negative interactions between them (Zobel, 1997; Reitalu *et al.*, 2008). Beta diversity β_w
181 (Whittaker, 1960) was calculated as the total number of plant species found in a given
182 site divided by the mean number of species in unit squares. We used it as an estimate of
183 mosaic heterogeneity of the plant cover.

184

185 Plant species were classified into several groups according to their growth
186 habits: mosses, grasses, forbs (non-grassy herbs), legumes (here only Fabaceae),
187 ericaceous shrubs, non-ericaceous shrubs, trees (here only oak) and lianas. The percent
188 occupancy of a given plant group per unit square was estimated by dividing the
189 maximum number of sub-units occupied by a species member of this group by the total
190 number of sub-units (25).

191

192 Ellenberg indices (Light, Moisture, Reaction and Nitrogen) were attributed to
193 each species (Table 2) using data for British vascular species (Hill *et al.*, 1999)
194 completed for moss species by online data (MAVIS 2000,
195 <http://www.ceh.ac.uk/products/software/mavis/download.asp>). Most identified species
196 were present in the British data base (Table 2). They were taken into account in the
197 calculation of average Ellenberg indicator values (Diekmann & Lawesson, 1999) per
198 unit square. Species were not weighted by percent occupancy, according to Wamelink
199 & Van Dobben (2003) and contrary to suggestions made by Diekmann (2003), because
200 we thought that the percent occupancy was too sensitive to growth habits, and may
201 confound habitat preferences. The same method was applied to the three strategies
202 Competitive ability, Stress tolerance and Ruderalness (Grime, 1987). Grime strategies
203 were also found in the MAVIS data base with the exception of moss species and some
204 vascular species (Table 2). Ellenberg indices were used to describe habitat preferences
205 and Grime strategies to describe life-history traits.

206

207 Correspondence analysis (CA) was used to discern trends in the distribution of
208 plant species across the 10 investigated sites (Greenacre, 1984). This indirect gradient
209 method was chosen because of its ease to discern trends in matrices of count numbers
210 (Benzécri, 1969; Kenkel, 2006). However, it was slightly improved, as explained below.
211 Species present in less than two samples were omitted from the analysis, because they
212 were not judged very informative. Species were coded as in Table 2 and their percent
213 occupancy in the different samples was used to built a data matrix crossing 79 species
214 as rows (active variables) and 105 samples as columns. Passive variables were added as
215 additional lines: soil (shallow or deep, each coded as 1 or 0), sites (10 sites, each coded

216 as 1 or 0), species richness per sample (number of species), growth habit occupancy
217 (eight types, each in percent), average Ellenberg indices (4) and Grime strategies (3) per
218 sample (each in percent). All variables (active and passive) were reweighted and
219 refocused (variance equal to 1 and mean equal to 20), in order to (i) avoid advantaging
220 rare species, (ii) interpret factorial coordinates of variables in terms of their contribution
221 to the axes and (iii) allow mixing data of varying type (Fédoroff *et al.*, 2005).
222 Additional variables with floating values were doubled ($X' = 40 - X$, X being the original
223 value, X' the new, conjugate value), each variable being represented by two points, one
224 for its higher values (original values), the other for its lower values (conjugate values),
225 symmetrical around the origin of the axes, with a gradient between them (Fédoroff *et al.*,
226 2005). The choice of 40 was justified by the need to avoid negative values, but it has no
227 effect on the calculation of eigen values.

228

229 The first axis of CA was used to measure the tolerance of the different plant
230 species to overall environmental influences, or niche width (McNaughton & Wolf,
231 1970). For each plant species the variance of CA coordinates along Axis 1 was averaged
232 over all samples, each sample being weighted by the percent occupancy of the species.
233 The higher was the variance the higher was the tolerance of the species to the
234 environmental variation depicted by Axis 1 of CA. The average tolerance of the plant
235 community or Tolerance Index (Dolédec *et al.*, 2000) was calculated by averaging the
236 unweighted tolerance value of the different plant species found in each sample.

237

238 Given that our data could be thought at first sight to be autocorrelated (samples
239 taken in the same site are not independent), correlation was tested by Signed Mantel
240 tests (Legendre & Legendre, 1998; Oberrath & Böhning-Gaese, 2001). For that purpose

241 geographical and ecological distance matrices were built. The ecological distance
242 between two samples was measured by the signed (algebraic) difference in the value of
243 a parameter (for instance the percent occupancy of a given species or group of species
244 or Axis 1 of CA). The correlation between two distance matrices was calculated as the
245 product-moment correlation coefficient, which was then tested by Monte-Carlo
246 simulation. Partial Mantel tests were used to discern possible causal relationships within
247 a set of self-correlated variables (Legendre & Fortin, 1989).

248

249 All statistical treatments were performed with XLStat Pro[®] version 2007.5
250 (Addinsoft[®]).

251

252 **Results and discussion**

253

254 Within-site spatial autocorrelation

255

256 Species richness of unit squares and percent occupancy of ericaceous vegetation were
257 used to test for the existence of within-site spatial autocorrelation (between-site
258 autocorrelation being considered trivial in our study). Only sites with a higher number
259 of unit squares (BP1 with 17 samples, BP2 with 20 samples and BNP with 29 samples)
260 were considered. Signed Mantel correlation coefficients r_M between geographic distance
261 and species richness showed a negative spatial autocorrelation of species richness in the
262 more pastured heath BP2 ($r_M = -0.21$, $P < 0.01$): nearby unit squares differed more than
263 null expectation, i.e. there was a mosaic of species-rich and species-poor zones at a
264 scale ~6-7m. A positive spatial autocorrelation was detected in the non-pastured heath
265 BNP ($r_M = 0.12$, $P < 0.05$), showing the existence of patches of species-rich and species-

266 poor vegetation at a scale in excess of 6-7m (nearby samples differed less than remote
267 samples). No spatial autocorrelation was detected in the slightly pastured heath BP1 (r_M
268 = 2.10^{-17} , $P = 0.98$), showing the absence of species-rich and species-poor vegetation
269 patches at least at the scale of the sampling grid ($\geq 6-7m$).

270

271 Contrary to species richness, the percent occupancy of ericaceous vegetation, as
272 well as that of *E. scoparia* alone, did not show any spatial autocorrelation at the scale of
273 the sampling grid.

274

275 The gradient of floristic composition depicted by Correspondence Analysis

276

277 Most significant variation in the floristic composition was depicted by Axis 1 (10% of
278 the total variation), along which all plant species were regularly distributed. Axis 2
279 (7.6% of the total variation) corresponded to only one sample taken in BP2, and thus
280 was not considered. Axis 1 correlated well with all vegetation parameters measured at
281 the community level (Table 1). Highest correlation values were with Tolerance Index
282 and Light Index, 60% and 52% of the total variation of which being depicted by Axis 1,
283 respectively (Fig. 2). The Light Index decreased while Moisture, Reaction and Nitrogen
284 Ellenberg indices increased when Axis 1 values increased. Grime strategies 'Stress
285 tolerance' and 'Ruderalness' decreased while 'Competitive' ability increased when Axis
286 1 values increased. Local species richness and beta diversity decreased when Axis 1
287 values increased. The percent occupancy of mosses, legumes, ericaceous and non-
288 ericaceous shrubs decreased while that of grasses, oak trees and lianas increased when
289 Axis 1 values increased. This was reflected in the projection of passive variables along
290 Axis 1 (Fig. 3). All vegetation parameters negatively correlated with Axis 1 were

291 projected on the negative (lower) side, while those positively correlated were projected
292 on the positive (upper) side, as expected. In addition, shallow soil was projected far
293 from the origin on the negative side, the contrary for deep soil, and the 10 sites were
294 classified in the following order, from negative to positive values of Axis 1: BP2 < BP1
295 < BNP < BA3 = BA2 <, BA1 = BSF2 < BSF1 = CHM1 < CHM2. We interpreted Axis
296 1 as a gradient of stability of the ecosystem, from pastured heath to oak-wood,
297 associated with increasing soil thickness and fertility, the latter being indirectly
298 ascertained from (i) Ellenberg indices (less light, more nitrogen, more moisture, less
299 acidity), (ii) Grime plant strategies (less ruderals and stressors, more competitors) and
300 (iii) niche width (increasing Tolerance Index of the community).

301

302 More woody species were projected on the positive side of Axis 1 (Fig. 4), while
303 more herb species were projected on the negative side of this axis. The increase in the
304 number of woody species and the decrease in the number of herb species along Axis 1
305 contrasts with the absence of any significant correlation between Axis 1 and percent
306 occupancy by forbs (Table 1, Fig. 3) and the weak (although significant) correlation
307 between Axis 1 and percent occupancy by grasses. This means that although more forbs
308 and grasses were present in more open environments (negative side of Axis 1), they
309 occupied more restricted areas than under higher vegetation (positive side of Axis 1),
310 thus giving them low scores of occupancy.

311

312 Two species of patrimonial interest were present in our samples: *Arenaria*
313 *montana* L., which is protected locally, and *Halimium umbellatum* (L.) Spach., which is
314 protected regionally (Pinet, 2005). Both species were projected far from the origin, on
315 the negative side of Axis 1, i.e. they were typically present in pastured heath. No

316 invasive species was found in the investigated sites, which are in a fairly good state of
317 naturalness (Pinet, personal communication).

318

319 It may be questioned whether the main gradient depicted by Axis 1 of CA was a
320 potential trajectory of the ecosystem (from pastured heath to oak forest) or the
321 juxtaposition of separate habitats. A nearby wet meadow with grasses and rushes was
322 excluded from our study because it did not exhibit any relationships with the vegetation
323 types used for our study, thereby restricting comparisons to well-drained sites with
324 varying soil depth. In the environmental conditions prevailing in the studied region,
325 lowland is commonly used for pasture and fish breeding, and sandstone outcrops
326 ('buttons') are abandoned to colonization by heath and oak-wood. The colonisation of
327 outcrops by oak can be observed whenever soils are at least 20 cm thick, i.e. when soils
328 were not completely destroyed by human activities (pasture, mining) or had time to
329 recover from naked bedrock (Rallet, 1935; Perrinet, 1995; Gaudillat, 1997). The same
330 successional trajectory may thus be arrested at different stages according to the (slow,
331 sometimes nil) soil development, like in a primary succession (Miles & Walton, 1993).
332 In that sense Axis 1 describes both a (potential) successional trajectory and a continuum
333 of habitats.

334

335 The effect of ericaceous vegetation, grazing and oak colonisation on plant biodiversity

336

337 Compared with other vegetation features, plant species richness did not display a good
338 relationship with the gradient depicted by Axis 1, despite a negative and highly
339 significant Mantel correlation coefficient (Table 1). However, on the negative side of
340 Axis 1, BNP, BP1 and BP2 form a sequence of increasing distance to the origin which

341 is related to an increasing level of grazing (nil in BNP, low in BP1, medium in BP2) and
342 an increasing level of species richness (Table 1). The three sites are on shallow soils, at
343 the top or near the top of Buttons A and B (Table 1). Species richness near doubled
344 from BNP to BP2, BP1 being intermediate, while the beta diversity β_w did not vary to a
345 great extent (Table 1). Other pronounced differences between non-pastured and
346 pastured heath were in the percent occupancy of grasses, which tripled from BNP to
347 BP2 (BP1 being intermediate) and ruderalness, which increased from BNP to BP1 then
348 to BP2 (Table 1). Plotted against the percent occupancy of ericaceous vegetation in
349 treeless sites, plant species richness showed a decreasing trend (Fig. 5), indicating that
350 in the absence of trees any decrease in ericaceous vegetation would increase plant
351 species richness. This is reflected in a negative and highly significant Mantel correlation
352 coefficient ($r_M = -0.54$, $P < 0.0001$) between species richness and percent occupancy by
353 ericaceous vegetation. The projection of individual samples from the same site (Fig. 5)
354 suggests that the decreasing trend displayed when all treeless sites are plotted together is
355 still depicted at the inside of individual sites, except in BA1, BA2 and BA3 (old heath)
356 where the percent occupancy by ericaceous vegetation is always high. The Mantel
357 correlation coefficient between species richness and percent occupancy by ericaceous
358 vegetation was negative and highly significant ($P < 0.0001$) in BNP ($r_M = -0.32$), BP1
359 ($r_M = -0.36$) and BP2 ($r_M = -0.43$). When all sites (oak-heath and oak-wood included)
360 were taken into account, the Mantel correlation coefficient between species richness and
361 percent occupancy by ericaceous vegetation was lower ($r_M = -0.25$) but still highly
362 significant ($P < 0.0001$). When corrected for percent occupancy by trees (oak), partial
363 r_M calculated on all sites became as low as -0.42 thus of the same magnitude as when
364 only treeless sites were considered.

365

366 Calculated on all sites, there was a very weak (although still highly significant)
367 negative effect of percent occupancy by oak on species richness ($r_M = -0.09$, $P <$
368 0.0001). When corrected for percent occupancy by ericaceous vegetation the negative
369 oak effect became much more prominent (partial $r_M = -0.36$, $P < 0.0001$) but remained
370 at a lower level than the negative effect of ericaceous vegetation when corrected for oak
371 effect (partial $r_M = -0.42$, $P < 0.0001$).

372

373 We showed that the species richness at the unit square (1m^2) level decreased in
374 parallel with the development of woody (shrub or tree) vegetation. Within the limits of
375 causality inference based on correlation values (Thagard, 1998), we interpret it as a
376 result of the detrimental effect of woody vegetation to the small-scale coexistence of
377 plant species, which has been observed to occur in wooded pastures (Gillet *et al.*, 1999).
378 This effect was more prominent with ericaceous than with oak cover and could be
379 attributed to a combination of factors such as competition for light and nutrients (Aerts
380 *et al.*, 1990) and mycorrhizal interference (Genney *et al.*, 2000). The nutrient status of
381 the soil improved along the environmental gradient from heath to oak-wood (Axis 1 of
382 CA), as ascertained from habitat preferences and life-history traits of plant species (Fig.
383 2, Table 1). Similar changes have been observed when ericaceous heath becomes
384 colonised by oak (Nielsen *et al.*, 1987, 1999). Thus, the observed decrease in plant
385 species richness under oak cannot be ascribed to scarcity of nutrients and increased
386 acidity (Roem & Berendse, 2000). Given that Grime's Competitive ability and
387 Tolerance Index of the community (mean niche breadth) increased along the
388 environmental gradient depicted by Axis 1 of CA while Stress Tolerance decreased, we
389 interpret the observed decrease in species coexistence level as a result of increased

390 exploitative competition rather than direct interference or environmental stress (Huston,
391 1979; Grime, 1985; Connell, 1990).

392

393 On shallow soils ('buttons'), we observed a favourable effect of grazing on
394 species coexistence level when comparing non-grazed heath (BNP) to slightly grazed
395 (BP1) and to moderately grazed heath (BP2). Grime's Ruderalness increased and
396 Competitive ability decreased from BNP to BP1 and BP2 (Table 1), thus pointing to an
397 alleviation of competition through herbivory (Bardgett *et al.*, 1998) and associated
398 disturbances known to favour non-ericaceous plant species such as trampling (Gallet &
399 Rozé, 2001; Kohler *et al.*, 2006) and dung deposition (Welch, 1985; Feeley, 2005).
400 Such a small-scale effect of grazing has been registered at a moderate level of cattle
401 pressure (Dupré & Diekmann, 2001), and was verified experimentally (Lavorel *et al.*,
402 1998). The explanation lies in an increase in spatial and temporal heterogeneity and
403 multi-scaling of the ecosystem at a moderate level of disturbance, known to favour the
404 coexistence of species (Denslow, 1985; Lavorel *et al.*, 1994; Levin, 2000), more
405 especially at the time of seedling establishment (Grubb, 1977). In the case of rocky
406 outcrops ('buttons') which are submitted to harsh climate conditions and poor nutrient
407 availability, most plants are stress tolerant (Table 1) and exhibit low nutrient loss rates
408 due to their evergreen habits (Aerts, 1995). They devote a prominent part of energy
409 requirements to resistance to environmental and biological hazards (Stowe & Osborn,
410 1980), this being reinforced in the presence of cattle grazing by the resistance of
411 seedlings and mature plants to herbivory (Coley *et al.*, 1985; Hanley, 1998). It must be
412 noted that species of patrimonial interest were also favoured by cattle grazing on
413 shallow soils.

414

415 Temporary but repeated grazing and trampling by cattle may thus be considered
416 as a factor allowing vegetation and soil to remain at a pioneer stage with a richer and
417 patrimonial flora (Partzch, 2007).

418

419 **Conclusion**

420

421 Our study, although limited in time and space, allowed us to describe a number of
422 vegetation types which are representative of rocky outcrops of the Brenne Regional
423 Natural Park, as ascertained from the extensive study done by Gaudillat (1997). We
424 showed that a variety of plant strategies and ecological traits could be found within a
425 limited area where natural (soil depth) and man-induced (cattle grazing) conditions
426 interfere to create a mosaic of environments. That such regional hot spots of
427 biodiversity must be protected is now out of dispute at the European level. More
428 problematic are the management rules which should be applied to protect them in the
429 long-term. We showed that the development of shrub (heath) and tree (forest)
430 vegetation induced a change in plant communities, shifting from stress-tolerant to
431 competitive species, and that moderate grazing allowed more species, and especially
432 those of patrimonial interest, to cohabit. Rather than prescribed fire and clear-cut
433 operations, which are known to induce severe environmental stresses to a lot of
434 organisms, thereby impoverishing communities in the long-term (Donegan *et al.*, 2001;
435 Lloret *et al.*, 2005), moderate grazing by cattle or sheep might be the best method for
436 the sustainable management of outcrop vegetation in agricultural landscapes, as this has
437 been successfully experimented in other regions (Pakeman *et al.*, 2003; Agreil & Greff,
438 2008).

439

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441

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446

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657 **Legends for figures**

658

659 **Figure 1.** Map of the study area and location of the 10 sites. a = BP1, b = BA1, c =

660 BP2, d = BNP, e = BA2, f = BA3, g = BSF1, h = BSF2, k = CHM2, m = CHM1

661

662 **Figure 2.** Relationship between Tolerance Index (Dolédec *et al.* 2000) and Ellenberg's

663 Light Index with the first axis of Correspondence Analysis (CA). Equations of

664 regression lines and determination coefficients are indicated. Codes for the 10

665 study sites as in Table 1

666

667 **Figure 3.** Projection of passive variables along Axis 1 of CA: sites (in boxes), soil types

668 (underlined), percent occupancy by species groups, average Ellenberg indices,

669 average Grime strategies and Tolerance Index (higher values in bold, lower

670 values in italics, see text for more details)

671

672 **Figure 4.** Projection of the 79 plant species along Axis 1 of CA. Species codes and

673 letter types as in Table 2

674

675 **Figure 5.** Relationship between percent occupancy by ericaceous vegetation and plant

676 species richness of unit samples, in 6 oak-free heath sites. Codes for sites as in

677 Fig. 1. Equation of regression line and determination coefficient are indicated

678

679

Table 1. Main site and vegetation features of the 10 investigated plots (mean \pm S.E). r_M is a Mantel correlation coefficient with Axis 1 values, tested by Monte-Carlo simulation. *** = significant at 0.001 level. NS = not significant at 0.05 level

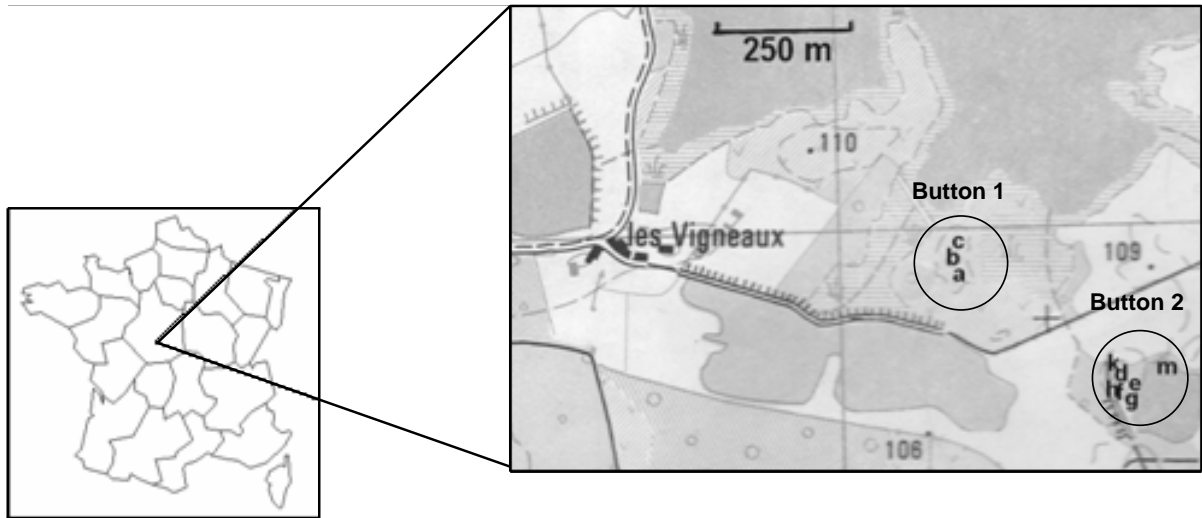
Code	BP2	BP1	BNP	BA3	BA2	BA1	BSF2	BSF1	CHM1	CHM2	r_M
Site (button)	1	1	2	2	2	1	2	2	2	2	
Vegetation type	Pastured heath	Pastured heath	Non-pastured heath	Old heath	Old heath	Old heath	Oak-heath	Oak-heath	Oakwood	Oakwood	
Soil type	Shallow	Shallow	Shallow	Deep	Deep	Deep	Deep	Deep	Deep	Deep	
Number of samples	20	17	29	4	5	10	5	5	5	5	
Species richness per m ²	14.4 \pm 0.9	12.6 \pm 1	7.9 \pm 0.4	7 \pm 0.7	7.2 \pm 0.9	11.6 \pm 0.9	7.6 \pm 1.2	11 \pm 1.9	7 \pm 0.8	11.6 \pm 1.7	-0.24***
Beta diversity (Whittaker's β_w)	3,8	3,4	3,7	1,9	2,4	2,8	2,6	2,7	2,1	2,2	
Mosses %	76.8 \pm 3.8	90.6 \pm 2.9	77.5 \pm 5	83 \pm 17	76 \pm 19.4	72.5 \pm 6.7	16.8 \pm 7.2	61.6 \pm 16.7	0.8 \pm 0.8	5.6 \pm 1.6	-0.60***
Grasses %	53.6 \pm 4.9	46.6 \pm 6	17.2 \pm 4.8	2 \pm 2	17.6 \pm 10.5	24.3 \pm 3.8	40 \pm 17.4	14.4 \pm 6	100 \pm 0	80.8 \pm 19.2	0.08***
Forbs %	43.4 \pm 5.8	41.4 \pm 5.1	15.6 \pm 4.4	5 \pm 3	16.8 \pm 8.2	30.1 \pm 7.6	19.2 \pm 6.4	10.4 \pm 7.1	75.2 \pm 15.3	48.8 \pm 5.6	0.01NS
Legumes %	67.6 \pm 6.5	58.4 \pm 7.6	51.7 \pm 5.5	17 \pm 5	9.6 \pm 5.5	1.7 \pm 0.8	2.4 \pm 1	2.4 \pm 1.6	3.2 \pm 2.3	2.4 \pm 2.4	-0.39***
Ericaceous shrubs %	56.2 \pm 5.5	62.6 \pm 7.5	85.5 \pm 3.5	95 \pm 5	88 \pm 10.1	87.5 \pm 0	20 \pm 20	45.6 \pm 20	0 \pm 0	0 \pm 0	-0.38***
Non-ericaceous shrubs %	66.4 \pm 7	67.5 \pm 5.6	58.2 \pm 4.7	75 \pm 25	9.6 \pm 3.5	44.8 \pm 6.7	2.4 \pm 1	8.8 \pm 4.6	0.8 \pm 0.8	15.2 \pm 8.3	-0.43***
Oak trees %	6.4 \pm 5.1	4.2 \pm 2.6	9.5 \pm 4.9	0 \pm 0	16.8 \pm 15.8	1.7 \pm 0.8	75.2 \pm 16.7	92 \pm 17.8	100 \pm 0	100 \pm 0	0.68***
Lianas %	1.2 \pm 1.2	8.7 \pm 4.9	5 \pm 2.8	5 \pm 3.8	0 \pm 0	6.1 \pm 3.9	14.4 \pm 7.4	22.4 \pm 10.5	75.2 \pm 12.4	41.6 \pm 11.8	0.58***
Light Index	7.3 \pm 0.05	7.27 \pm 0.05	7.31 \pm 0.06	7.17 \pm 0.15	7.1 \pm 0.07	6.71 \pm 0.07	6.58 \pm 0.27	6.51 \pm 0.14	6.13 \pm 0.13	6.31 \pm 0.12	-0.72***
Moisture Index	5.35 \pm 0.08	5.22 \pm 0.11	5.81 \pm 0.04	6.01 \pm 0.3	5.71 \pm 0.18	5.45 \pm 0.08	5.54 \pm 0.14	5.48 \pm 0.11	5.28 \pm 0.13	5.48 \pm 0.08	0.14***
Reaction Index	3.89 \pm 0.09	4.13 \pm 0.1	3.58 \pm 0.08	4.59 \pm 0.15	4.47 \pm 0.23	4.77 \pm 0.08	4.55 \pm 0.21	4.63 \pm 0.1	4.75 \pm 0.17	4.86 \pm 0.22	0.5***
Nitrogen Index	2.58 \pm 0.1	2.93 \pm 0.08	2.49 \pm 0.09	3.33 \pm 0.16	3.26 \pm 0.13	3.44 \pm 0.08	3.71 \pm 0.27	3.63 \pm 0.19	4.17 \pm 0.21	4.3 \pm 0.19	0.7***
Competitive ability	1.97 \pm 0.04	2.01 \pm 0.06	2.35 \pm 0.8	3.08 \pm 0.08	2.72 \pm 0.12	2.82 \pm 0.08	2.99 \pm 0.14	2.73 \pm 0.14	2.92 \pm 0.05	2.96 \pm 0.04	0.7***
Stress tolerance	3.53 \pm 0.08	3.18 \pm 0.07	3.63 \pm 0.08	2.75 \pm 0.16	3.32 \pm 0.14	3.11 \pm 0.05	3.01 \pm 0.14	3.17 \pm 0.11	2.8 \pm 0.12	2.77 \pm 0.06	-0.45***
Ruderalness	1.88 \pm 0.11	2.34 \pm 0.11	1.12 \pm 0.04	1.42 \pm 0.25	1.45 \pm 0.14	1.83 \pm 0.1	1.6 \pm 0.21	1.39 \pm 0.06	1.83 \pm 0.09	1.98 \pm 0.14	-0.11***
Tolerance Index	0.42 \pm 0.02	0.49 \pm 0.02	0.46 \pm 0.02	0.54 \pm 0.04	0.62 \pm 0.05	0.63 \pm 0.02	1.05 \pm 0.09	0.79 \pm 0.1	1.1 \pm 0.03	1.01 \pm 0.01	0.77***
Axis 1 of CA	0	-0.62 \pm 0.14	-0.26 \pm 0.05	0.11 \pm 0.02	0.15 \pm 0.07	0.64 \pm 0.1	0.84 \pm 0.1	1.42 \pm 0.69	1.46 \pm 0.24	2.2 \pm 0.24	

680

681

Table 2. Code and latin name of plant species recorded in the study area in at least two samples, together with their tolerance values, Ellenberg values and CSR strategies when known. Codes in bold type for vascular species (lower case for herbs, upper case for trees and shrubs), in italic lower case type for mosses and lichens, underlined for legumes

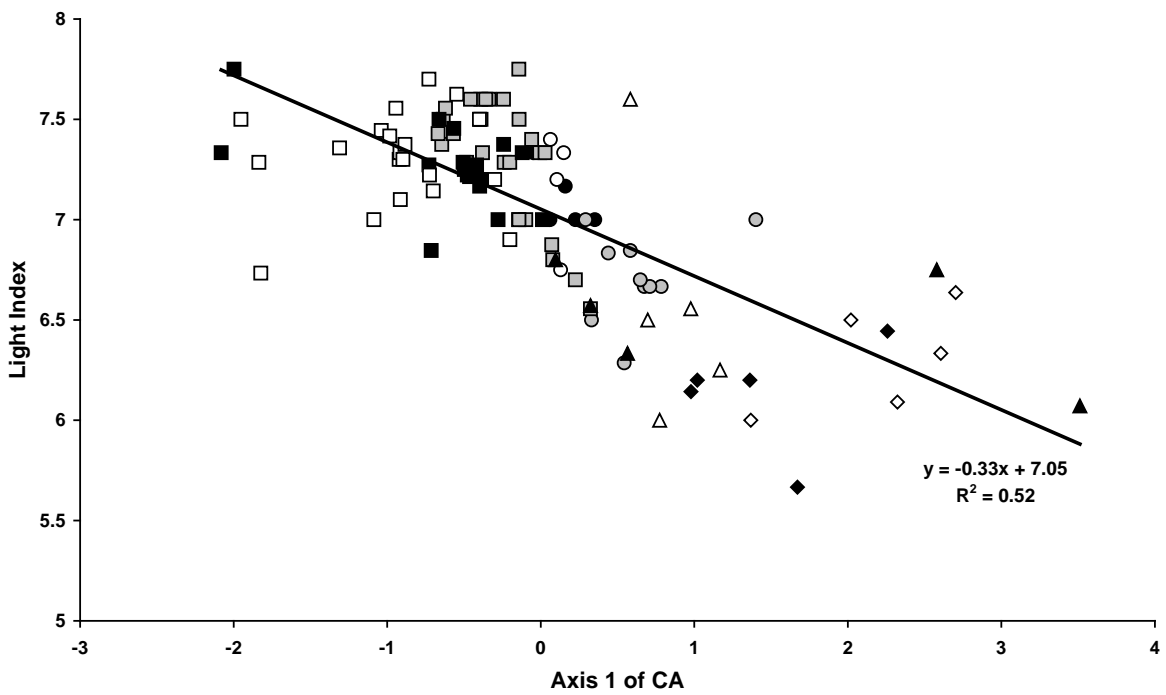
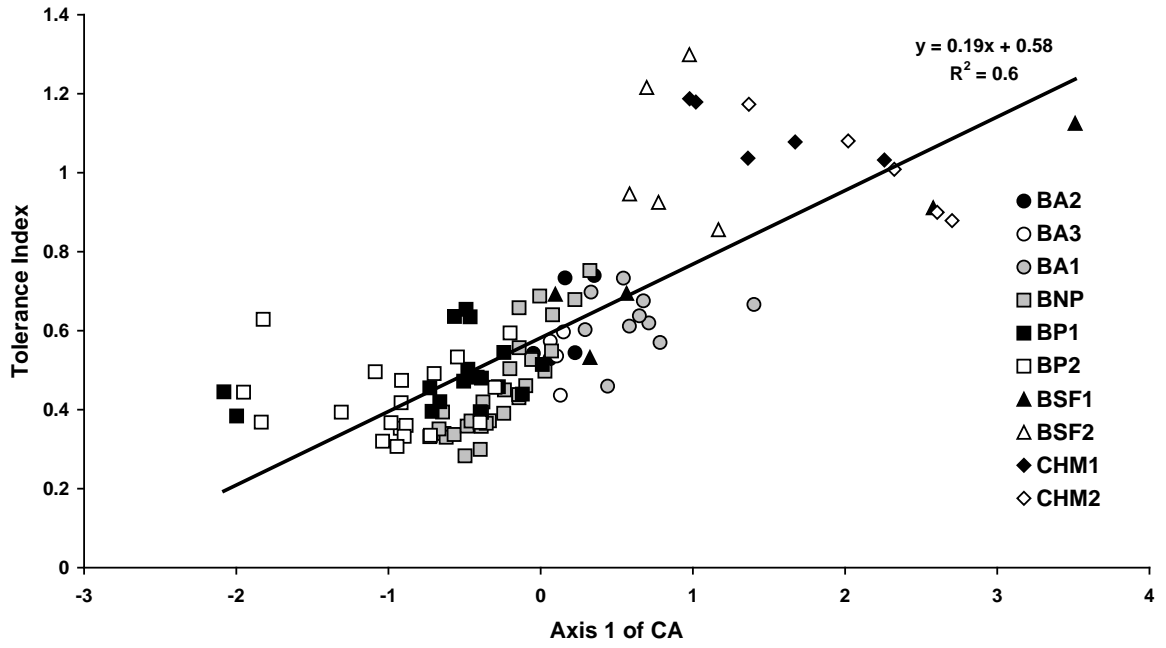
Code	Latin name	Light	Moisture	Reaction	Nitrogen	Competitive ability	Stress-tolerance	Ruderalness	Tolerance value
amo	<i>Arenaria montana</i> L.								0.37
aod	<i>Anthoxanthum odoratum</i> L.	7	6	4	3	2	3	3	0.90
apr	<i>Aira praecox</i> L.	8	2	4	2	1	3	3	0.41
ate	<i>Agrostis tenuis</i> Sibth.	6	5	4	4	3	3	3	0.95
aun	<i>Atrichum undulatum</i> (Hedw.) P. Beauv.	7	6	3	4				1.02
bca	<i>Bryum caespitium</i> Hedw.								0.00
bru	<i>Brachythecium rutabulum</i> (Hedw.) B., S. & G.	6	5	6	5				0.35
bsp	<i>Bryum</i> sp.	7	5	7	7				0.14
bsu	<i>Bryum subapiculatum</i> Hampe								0.12
cgl	<i>Cerastium glomeratum</i> Thuill.	7	5	6	5	1	2	4	0.20
CMO	<i>Crataegus monogyna</i> Jacq.	6	5	7	6	3	3	1	1.37
cpi	<i>Carex pilulifera</i> L.	7	5	3	2	1	5	1	0.27
cpu	<i>Ceratodon purpureus</i> (Hedw.) Brid.	5	5	4	5				0.21
CSC	<i>Cytisus scoparius</i> (L.) Link	8	5	4	4	3	3	1	1.50
cs1	<i>Carex</i> sp.								0.00
cs2	<i>Cerastium</i> sp.	8	3	7	4				0.31
CVU	<i>Calluna vulgaris</i> (L.) Hull	7	6	2	2	3	3	1	0.18
dde	<i>Danthonia decumbens</i> (L.) DC.	7	6	4	2	1	5	1	0.01
dhe	<i>Dicranella heteromalla</i> (Hedw.) Schimp.	9	3	4	1				0.73
dsc	<i>Dicranum scoparium</i> Hew.	9	3	4	1				0.21
ECl	<i>Erica cinerea</i> L.	7	5	2	2	2	4	1	0.31
ESC	<i>Erica scoparia</i> L.								0.55
est	<i>Eurhynchium striatum</i> (Hew.) Schimp.	7	5	4	3				0.12
FAL	<i>Frangula alnus</i> Mill.	6	8	5	5				0.00
fbr	<i>Fissidens bryoides</i> Hedw.								0.22
fov	<i>Festuca ovina</i> L.	7	5	4	2	1	5	1	0.23
GAN	<i>Genista anglica</i> L.	8	5	3	2				0.00
gap	<i>Galium aparine</i> L.	6	6	7	8	3	1	3	0.12
gmo	<i>Geranium molle</i> L.	7	5	6	5	1	2	4	0.36
hcu	<i>Hypnum cupressiforme</i> Hedw.	8	8	4	2				1.01
HHE	<i>Hedera helix</i> L.	4	5	7	6	3	3	1	1.00
hhu	<i>Hypericum humifusum</i> L.	7	6	4	3	2	4	2	0.89
him	<i>Hieracium umbellatum</i> L.								0.05
hju	<i>Hypnum jutlandicum</i> Balcerk. et Brzeg	8	8	4	2				0.41
hla	<i>Holcus lanatus</i> L.	7	6	6	5	3	3	3	0.11
hlm	<i>Hypnum lacunosum</i> (Brid.) Hoffm. ex Brid.								0.32
hmo	<i>Holcus mollis</i> L.	6	6	3	3	4	2	2	1.05
hpi	<i>Hieracium pilosella</i> L.	8	4	7	2				0.38
hra	<i>Hypochoeris radicata</i> L.	8	4	5	3	3	3	3	0.34
hum	<i>Halimium umbellatum</i> (L.) Spach.								0.26
jsp	<i>Juncus</i> sp.	7	8	4	3				0.28
kpr	<i>Kindbergia praelonga</i> (Hedw.) Ochyra	7	5	4	3				0.56
lca	<i>Luzula campestris</i> (L.) DC.	7	4	5	2	2	4	2	0.50
LPE	<i>Lonicera periclymenum</i> L.	5	6	5	5				1.10
lsp	Unidentified lichen species								0.34
lvu	<i>Linaria vulgaris</i> Mill.	7	4	8	6	3	1	3	0.45
mmi	<i>Medicago minima</i> L.	9	3	7	2				1.36
mmr	<i>Montia minor</i> C. C. Gmel.	7	8	5	3	1	2	4	0.31
pan	<i>Poa annua</i> L.	7	5	6	7	1	1	5	0.32
pfo	<i>Polytrichum formosum</i> Hew.	4	5	6	6				0.33
pju	<i>Polytrichum juniperinum</i> Hew.	4	5	6	6				1.04
pla	<i>Plantago lanceolata</i> L.	7	5	6	4	3	3	3	0.57
ppr	<i>Poa pratensis</i> L.	7	5	6	6	3	3	3	0.03
pre	<i>Potentilla reptans</i> L.	7	5	7	5	3	2	3	0.00
pse	<i>Polygala serpyllifolia</i> Hose	8	7	2	2				0.02
PSP	<i>Prunus spinosa</i> L.	6	5	7	6	3	3	1	1.15
QHY	<i>Quercus</i> (hybrid)								0.79
QPE	<i>Quercus petraea</i> (Mattuschka) Lieblein	6	6	3	4	3	3	1	1.61
QPU	<i>Quercus pubescens</i> Willd.								0.64
QRO	<i>Quercus robur</i> L.	7	5	5	4	3	3	1	1.37
QSE	<i>Quercus</i> (seedling)								0.89
rac	<i>Rumex acetosella</i> L.	7	5	4	3	2	3	3	0.93
RAR	<i>Rosa arvensis</i> Huds.	6	4	7	5				0.00
rbu	<i>Ranunculus bulbosus</i> L.	7	4	7	4	1	3	3	0.21
RCA	<i>Rosa canina</i> L.	6	5	7	6				0.03
RFR	<i>Rubus fruticosus</i> L.	6	6	6	6	3	3	1	0.93
rla	<i>Racomitrium lanuginosum</i> J. H. Tallisl.	7	5	5	4				0.35
RSA	<i>Rubus</i> sp. A								0.31
RSB	<i>Rubus</i> sp. B								0.05
RSC	<i>Rubus</i> sp. C								0.09
spu	<i>Scleropodium purum</i> (Hedw.) Limpr.	8	5	6	2				0.63
sti	<i>Serratula tinctoria</i> L.	7	6	6	2				0.00
STO	<i>Sorbus torminalis</i> (L.) Crantz	4	5	6	5				0.21
tnu	<i>Teesdalia nudicaulis</i> (L.) R.	8	3	2	2				0.58
tsc	<i>Teucrium scorodonia</i> L.	6	4	4	3	2	4	2	1.30
UNA	<i>Ulex nanus</i> T. F. Forster ex Symons	8	6	1	2				0.24
vca	<i>Viola canina</i> L.	8	4	5	2				0.30
vch	<i>Veronica chamaedrys</i> L.	6	5	6	5	3	3	3	0.29
vsp	Unidentified vascular species								



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684 Fig. 1

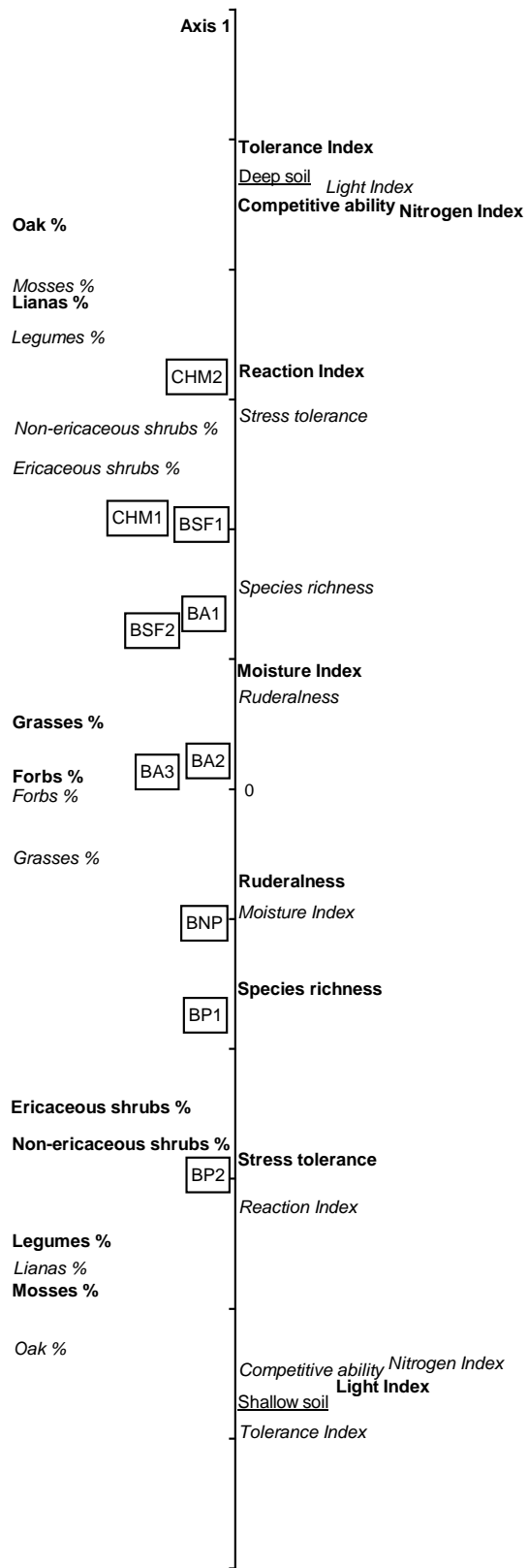
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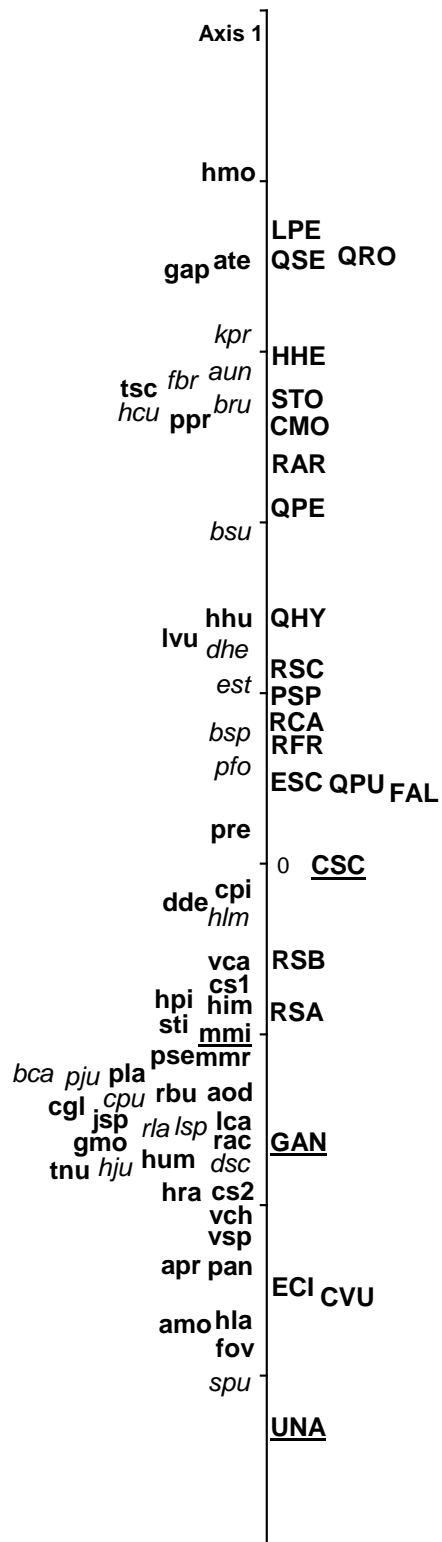
687 Fig. 2

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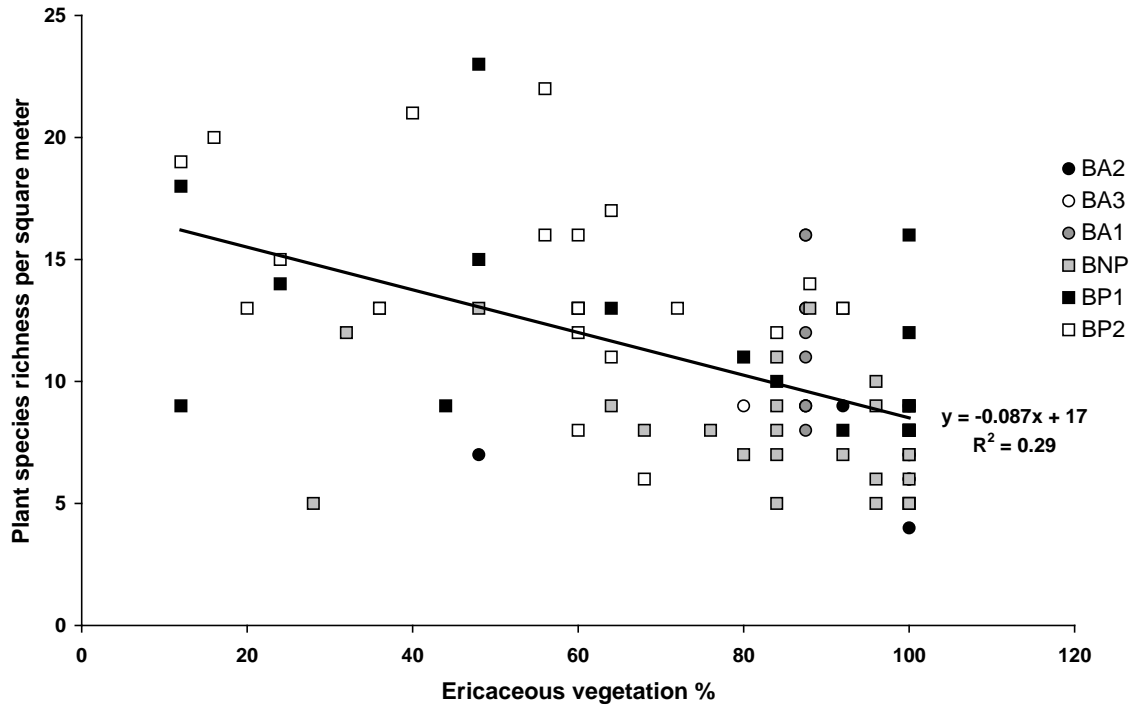
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690 Fig. 3



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692 Fig. 4



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694 Fig. 5