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This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1650731> since 2018-04-05T20:30:36Z

Published version:

DOI:10.1080/17550874.2017.1393703

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This is an author version of the contribution published on:

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[Plant Ecology & Diversity, 2017, 4, 343-351]

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The definitive version is available at:

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[<http://www.tandfonline.com/doi/full/10.1080/17550874.2017.139370>

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13 **Species-rich *Nardus stricta* grasslands host a higher vascular plant diversity on calcareous**
14 **than on siliceous bedrock**

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23

24 **Abstract**

25 **Background:** Species-rich *Nardus stricta* grasslands are a priority habitat for conservation in
26 Europe. They typically occur on siliceous substrates and less frequently are found on calcareous
27 bedrock.

28 **Aims:** The present paper aimed to identify the environmental factors (i.e. bedrock type,
29 topographic, and climatic factors) that are related with community diversity and to assess if
30 differences in plant diversity between *N. stricta* communities on calcareous and siliceous
31 bedrock occur. We hypothesised that *Nardus* grasslands on calcareous bedrock hosted a higher
32 vascular plant diversity than those on siliceous bedrock.

33 **Methods:** Based on 579 vegetation surveys carried out in the south-western Alps, we assessed
34 vascular plant diversity (species richness, Shannon diversity, and Pielou's equitability index) of
35 species-rich *Nardus* grasslands and compared it between *N. stricta* communities on calcareous
36 and siliceous bedrock.

37 **Results:** Elevation was identified as the main factor related to species composition, while
38 species diversity was mostly related to mean annual precipitation and bedrock type. Species
39 richness, Shannon diversity, and Pielou's equitability index were higher within the communities
40 on calcareous rather than on siliceous bedrock and a total of 89 and 34 indicator species were
41 detected, respectively.

42 **Conclusions:** Based on our results, we suggest to protect primarily, as a habitat of priority
43 interest, *N. stricta* grasslands on calcareous substrates for the higher vascular plant diversity
44 hosted.

45 **Keywords:** calcareous substrate; indicator species; Pielou's equitability index; Shannon
46 diversity index; siliceous substrate; species richness

47

48

49 **Introduction**

50

51 Due to their high vascular plant diversity, species-rich *Nardus stricta* grasslands are recognised
52 by the European Habitat Directive (92/43/EEC) as a habitat of priority interest. Specifically,
53 they are defined as ‘Species-rich *Nardus* grasslands, on siliceous substrates in mountain areas
54 (and submountain areas, in continental Europe)’ (habitat code 6230*). *Nardus* grasslands are
55 widespread in Europe, occurring over about 1918 km² within Natura 2000 sites in 24 countries
56 (Galvnek and Jank 2008). They occur across wide elevation and moisture gradients, from
57 Atlantic lowlands up to the mountain areas of continental Europe, such as the Alps, Apennines,
58 Carpathians, and Pyrenees (Galvnek and Jank 2008; Gennai et al. 2014). As a consequence of
59 the wide spectrum of ecological conditions in which they are found, *N. stricta* grasslands
60 encompass a large variety of different communities. The Italian Interpretation Manual of
61 Directive 92/43/EEC (Biondi et al. 2009) associates habitat 6230* to the following
62 phytosociological alliances occurring in the montane belt: *Violion caninae*, *Nardo-Agrostion*
63 *tenuis*, and *Ranunculo-Nardion*, belonging to the order *Nardetalia strictae* (*Nardetea strictae*
64 class). Moreover, the habitat includes the *Nardion strictae* (*Caricetea curvulae* class)
65 communities located in the sub-alpine belt, while *N. stricta* communities in the alpine belt (i.e.
66 the ones developed above the tree line) are attributed to habitat 6150 (‘Siliceous alpine and
67 boreal grasslands’).

68 Even if the Directive 92/43/EEC expressly indicates that species-rich *Nardus* grasslands
69 occur on siliceous substrates, without any reference to the calcareous ones, these communities
70 do occur also on calcareous bedrock, where precipitation has leached calcium from the top soil
71 (Galvnek and Jank 2008; Ellenberg 2009; Biondi et al. 2012). Such conditions have been
72 reported in Austria (Luth et al. 2011), France (Bensettiti et al. 2005), Slovakia (Stanov and
73 Valachovi 2002), Spain (Sebasti 2004), and Italy, both in the Alps and in the northern
74 Apennines (Gennai et al. 2014). In general, calcareous bedrock can harbour a high number of
75 plant species (Wohlgemuth 1998, 2002; Ewald 2003; Marini et al. 2008); however, the vascular

76 plant composition of *Nardus* grasslands on calcareous and siliceous bedrocks has never been
77 compared. Based on a large dataset collected over a broad area of the south-western Alps,
78 representative of different environmental gradients, the present paper tests the hypothesis that
79 *Nardus* grasslands on calcareous bedrock host a higher vascular plant diversity than those on
80 siliceous bedrock by (1) identifying which environmental factors (i.e. bedrock type, topographic
81 and climatic factors) mainly affect *Nardus* grassland plant diversity and (2) comparing plant
82 diversity between *N. stricta* communities on calcareous and siliceous bedrocks.

83

84 **Material and methods**

85 *Study area*

86 The study was carried out on the *N. stricta*-dominated communities of the Piedmont region,
87 western Italian Alps (Figure 1). In this broad area of the Alps, 92 different grassland types cover
88 more than 187,000 ha, of which 12% is dominated by *N. stricta* (Argenti and Lombardi 2012;
89 Cavallero et al. 2007). The grasslands are mostly used as summer pastures (Cavallero et al.
90 2007). Total annual precipitation ranges from continental regimes with 760 mm in the western
91 part of the study area to sub-oceanic regimes with 2400 mm in the northern part (i.e. the
92 ‘Insubric district’). Generally, precipitation decreases from the external to the internal sectors of
93 the valleys and follows a bimodal distribution, with spring and autumn peaks (Biancotti et al.
94 1998). Soils are developed on siliceous (about 70%; mainly gneiss and granite) and calcareous
95 bedrock (ca. 30%; mainly calc-schists, dolomite, and limestones) (Regione Piemonte 2006).

96 *Vegetation and environmental data*

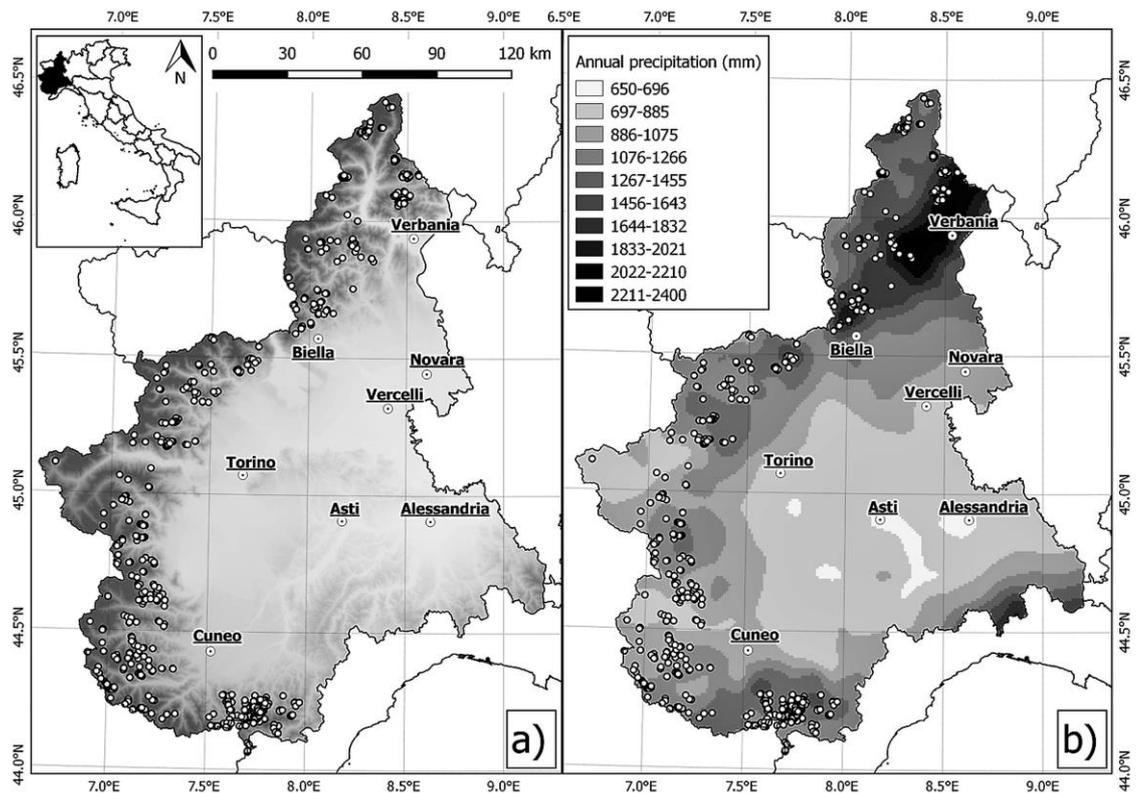
97 *Vegetation data.* During the period 2001–2007, 3888 25-m transects were recorded for vascular
98 plant composition by using the point-quadrat method (Daget and Poissonet 1971) In each
99 transect, at every 50-cm interval, plant species touching a steel needle were identified and
100 recorded. Since rare species are often missed by this method, a complete list of all other plant

101 species included within a 1-m buffer area around the transect line (i.e. the ‘vegetation plot’,
102 having a 50-m² area) was also recorded. The frequency of occurrence of each plant species,
103 which is an estimate of species canopy cover, was converted to percentage cover (Pittarello et
104 al. 2016). Moreover, the species relative abundance (SRA) was determined in each transect to
105 detect the proportion of different species according to the following equation (1) :

106
$$SRA_i = \frac{f_i}{\sum_{i=1}^n f_i} \times 100(\%) \quad (1)$$

107 where SRA_i and f_i are the species relative abundance and the frequency of occurrence of the
108 species i , respectively (Daget and Poissonet 1971). To all occasional plant species found within
109 vegetation plots and not along the linear transect a SRA value of 0.3 was attributed (Vacchiano
110 et al. 2016). The phytosociological optimum was associated to each plant species according to
111 Aeschimann et al. (2004).

112 Within this dataset, 579 samples were assigned to habitat 6230* following a two-step
113 selection. First, we selected *Nardus*-dominated grasslands when *N. stricta* percentage cover was
114 higher than 25%, according to the threshold used by Illyés et al. (2007). Second, to exclude the
115 *Nardus*-dominated grasslands ascribable to habitat 6150, we retained only those surveys located
116 at the montane and sub-alpine belts, according to the Italian Interpretation Manual of Directive
117 92/43/EEC (Biondi et al. 2009) (Figure 1a).



118

119 **Figure 1.** (a) Distribution of *Nardus* grasslands belonging to habitat 6230* in the Alpine
 120 chain of Piedmont region (represented on Digital Terrain Model). (b) Mean total annual
 121 precipitation map of Piedmont region.

122

123 We attributed the samples to the alpine or sub-alpine/montane belts depending on
 124 whether their elevation was higher or lower than the interpolated tree line limit computed for the
 125 latitude at which the survey was carried out. Since the elevation limit between the sub-alpine
 126 and alpine belt (i.e. the tree line limit) linearly changes with latitude (Ozenda 1985), we set the
 127 tree line limit with a linear interpolation from the southern zone of Piedmont (tree line at 2300
 128 m a.s.l. – 43.5° latitude) to the northern one (2000 m a.s.l. – 46.5° latitude), which corresponds
 129 to elevation and latitude limits set by Ozenda (1985).

130 We computed species richness, Shannon diversity (hereafter ‘H’), and Pielou’s equitability
 131 index (hereafter ‘J’ = H/H'_{max} , Pielou 1975), based on SRA values for each species in each
 132 sample. Floristic nomenclature followed Pignatti et al. (1982).

133 *Environmental data.* For each sample we computed topographic and climatic variables and
134 mean R Landolt indicator value for soil reaction (Landolt et al. 2010), which is a proxy for soil
135 pH (Orlandi et al. 2016). The R value was calculated by averaging species values weighted by
136 their SRA (Ravetto Enri et al. 2016). Topographic variables (elevation, slope, and aspect) were
137 determined from a 50-m resolution digital elevation model (Piemonte CSI 2005). Aspect was
138 transformed into southness ($\text{southness} = 180 - |\text{aspect} - 180|$) to avoid circular variable issues
139 (Chang et al. 2004). A 5-km resolution raster grid derived from long-term datasets of 521
140 weather stations spread over the Piedmont region (Biancotti et al. 1998) supplied total mean
141 annual precipitation (Figure 1b). To provide a general estimate of large-scale climatic patterns,
142 we used Gams' continentality index, calculated as the arctan of the ratio between precipitation
143 (P) and elevation (A) (Ozenda 1985).

144 Based on geological maps (Regione Piemonte 2006), samples were attributed to
145 calcareous or siliceous bedrock types. Spatial analyses were carried out with the software
146 Quantum GIS (Quantum GIS 2016, <http://qgis.osgeo.org>).

147 *Data analysis*

148 Multivariate relations between environmental variables and vegetation composition were
149 evaluated by a canonical correspondence analysis (CCA), using CANOCO 4.5 (ter Braak and
150 Šmilauer 2012). Being R Landolt indicator value computed from vegetation composition, it was
151 not included in the CCA to avoid a mathematical dependence with the ordination scores (Wildi
152 2016). Statistical significance of canonical axes was assessed by using the Monte Carlo test
153 (499 permutations). The species percentage cover data were $\log(x+1)$ -transformed before
154 analysis and rare species (i.e. species with a low frequency) were down-weighted to reduce their
155 effect on the other plant species distribution in the ordination diagram (Šmilauer and Lepš
156 2003). Pearson's correlation was computed between topographic and climatic variables and the
157 first and second axes of CCA.

158 Relationships among species richness, H' , and J' and environmental data were modelled
159 by fitting Generalised Linear Models (GLMs, Zuur et al. 2009). Species richness, H' , and J'

160 were used as dependent variables, whereas environmental data as explanatory variables. Since
161 species richness was a count overdispersed variable, a negative binomial distribution was
162 specified (overdispersion was tested with the *qcc* R package, according to Scrucca 2004).
163 Gamma distribution was set for Shannon diversity index, being it a not-normally distributed
164 continuous variable with positive values (normality was tested with Shapiro-Wilk test), while J'
165 was modelled with a Beta distribution, as it assumes values in the standard unit interval (0,1)
166 (Cribari-Neto and Zeileis 2010). Highly collinear predictors ($r > |0.70|$) were excluded after a
167 correlation analysis of environmental data. Since Gams' continentality index was positively
168 correlated with elevation ($r = 0.80$) and negatively correlated with total annual precipitation ($r =$
169 -0.91), it was excluded from subsequent analyses. To analyse the size of each effect by
170 comparing model parameter estimates (β -coefficients), explanatory variables were standardised
171 (Z-scores). Generalised Linear Models were carried out using the glmm ADMB package
172 (Fournier et al. 2012) in the R v. 3.2.3 environment (R Development Core Team 2015).

173 To assess differences in species richness, H' , and J' between calcareous and siliceous
174 bedrock surveys, Mann–Whitney U tests were performed with the 'wilcox.test' R function, as
175 assumptions for parametric t-tests were not met even after the transformation of variables.

176 An Indicator Species Analysis was used to identify specific plant species associated to
177 calcareous and siliceous bedrocks. The analysis was performed following the original Indicator
178 Value (IndVal) function of Dufrêne and Legendre (1997) by using the 'multipatt' function of
179 the 'indicspecies' package of R (De Cáceres and Legendre 2009). The IndVal is an index to
180 measure the association between a species and a group (calcareous or siliceous bedrock); it is
181 higher for species occurring in only one group (specificity) and with a high-abundance rate in
182 all the samples belonging to that group (fidelity). The statistical significance of the association
183 of a species with a group was obtained by 999 permutations. Differences between samples on
184 calcareous and siliceous bedrock in their proportion of indicator species associated to the
185 phytosociological classes typical of acidic (*Juncetea trifidi* and *N. strictae*) or calcicole swards
186 (*Elyno-Seslerietea variaie*) were assessed with a χ^2 -test on a contingency table.

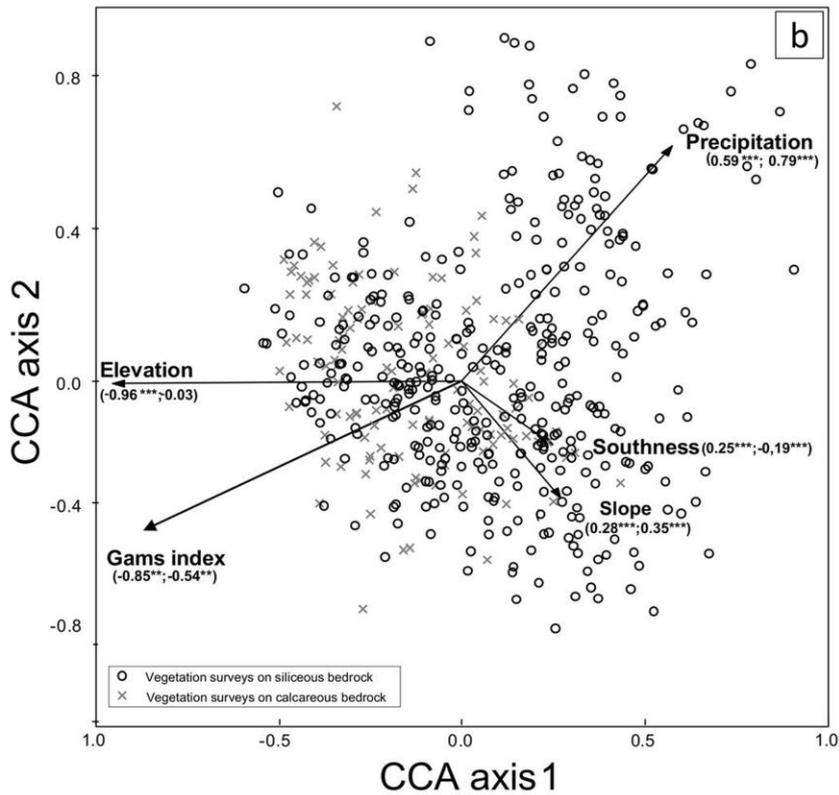
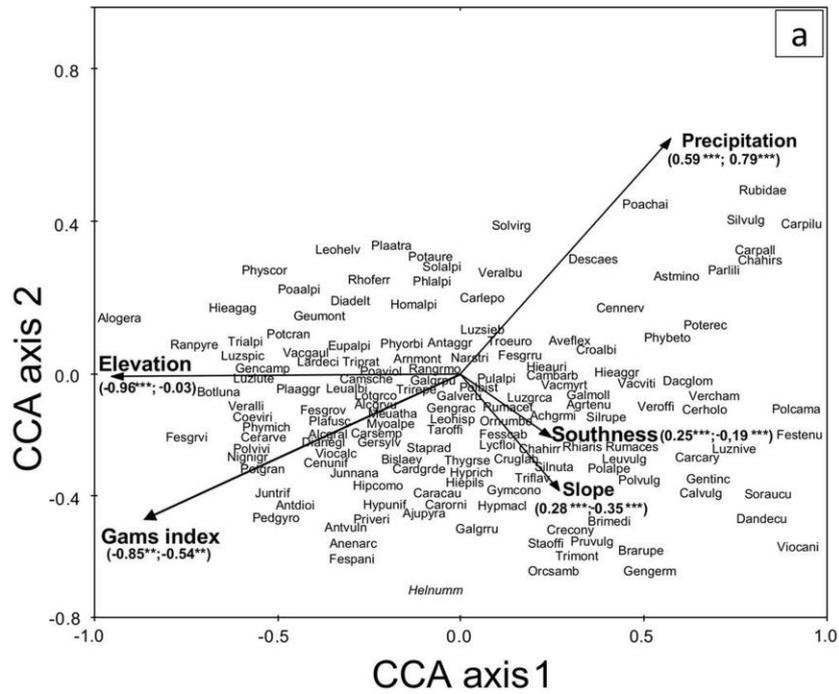
187

188 **Results**

189

190 We recorded a total of 540 plant species. The samples had a high variability in species richness,
191 H' , J' , and environmental conditions (Table 1), underlying the wide ecological spectrum in
192 which they occur. In particular, the mean Landolt soil reaction value (R) varied between 1.29
193 and 3.04, a range typical of vegetation communities growing from extremely to weakly acidic
194 soils. Moreover, 374 samples out of 579 (64.6%) belonged to siliceous bedrock and 205
195 (35.4%) were recorded on calcareous bedrock.

196 The total variance explained by axes 1 and 2 of CCA amounted to 80.7% (Monte-Carlo
197 test: $F = 11.02$, $P = 0.002$). The CCA ordination diagram (Figure 2a) showed a predominant
198 spatial gradient along axis 1, explaining 56.6% of the total variance. Along this axis, vegetation
199 composition was mainly affected by elevation (Pearson's correlation coefficient $R_p = -$
200 0.96^{***}), but also Gams' continentality index and precipitation were important factors ($R_p =$
201 0.85^{**} and 0.59^{***} , respectively). The communities occurring at the highest elevations were
202 dominated by species having their phytosociological optimum within the classes *J. trifidi* (e.g.
203 *Alopecurus gerardi* Vill., *Luzula spicata* (L.) DC, and *Ranunculus pyrenaicus* L.) and *Elyno-*
204 *Seslerietea varia* (e.g. *Festuca gr. ovina*, *Festuca gr. violacea*, and *Potentilla crantzii* (Crantz)
205 Beck). At lower elevations and with higher amount of precipitation, species having their
206 phytosociological optimum within the class *N. strictae* prevailed (e.g. *Carex pilulifera* L., *Carex*
207 *pallescens* L., and *Potentilla erecta* (L.) Rauschel). Eutrophic species, e.g. *Dactylis glomerata*
208 L., *Cerastium holosteoides* Fries, and *Galium mollugo* L., were associated with lower
209 elevations. Aspect and slope were less important factors to explain differences in vegetation
210 composition, as they were less correlated to the first and second axes of the CCA. Vegetation
211 composition did not distinctly separate calcareous and siliceous bedrock samples, due to the
212 overlapping of calcareous bedrock surveys within the multivariate ecological space of siliceous
213 bedrock surveys (Figure 2b).



214

215 **Figure 2.** (a) species-environmental variable biplot ordination diagram of the Canonical
 216 Correspondence Analysis (CCA). Only species occurring in more than 5% of 579 vegetation
 217 surveys are represented. Species codes and their attribution to the phytosociological optimal

218 class are reported in the Appendix. Pearson's linear correlation coefficient (R_P) and significance
219 between each ecological variable and the first and second axes are reported within brackets,
220 respectively. (b) vegetation survey-environmental variable biplot ordination diagram of the
221 CCA.

222

223 According to the standardised beta coefficients of GLMs, total annual precipitation and
224 bedrock type were the two most influential factors affecting species richness, H' , and J' (Table
225 2). Increasing annual precipitation was associated with lower values of species richness, H' and
226 J' , which instead increased on calcareous bedrock. Species richness and H' were higher at lower
227 elevations, whereas J' was not influenced by elevation. Vascular plant diversity was higher on
228 steeper slopes.

229 Samples on calcareous bedrock were characterised by a higher number of plant species
230 (seven species more, on average), H' , and J' , with a more even distribution of species
231 percentage covers, than those on siliceous bedrock (Table 3).

232 The indicator species analysis identified 34 species significantly associated with
233 samples on siliceous bedrock and 89 with the calcareous bedrock (Appendix). The main
234 difference between these two groups was related to the proportion of calcicole species, i.e.
235 species having the phytosociological optimum in the *Elyno-Seslerietea* class, that were
236 exclusive of *Nardus* grasslands on calcareous bedrock (Table 4).

237

238 **Discussion**

239

240 The high variability in topographic and climatic variables and bedrock type markedly affected
241 species richness, H' , and J' of the *Nardus* grasslands. Elevation explained most of *N. stricta*
242 community composition and negatively influenced both species richness and H' , as highlighted
243 by literature on other plant communities (Moser et al. 2005; Nogués-Bravo et al. 2008).
244 However, since the proportion of species with different percentage cover was rather stable at

245 different elevations, it did not affect the evenness of vegetation community. Moreover, elevation
246 was not amongst the most important variables influencing plant diversity, which was instead
247 mostly affected by mean annual precipitation and bedrock type. All the biodiversity parameters
248 showed the highest values within the locations with lower precipitation, typically associated to
249 the inner-alpine valleys of the Alpine chain, as also the negative relationship between
250 precipitation and Gams' continentality index confirmed. A higher water availability, associated
251 with frequent and abundant rainfall typical of sub-oceanic areas, determines optimal conditions
252 for the growth of *N. stricta*, which results in an increase in its dense litter layer and
253 competitiveness against other plant species (Chadwick 1960). Moreover, high precipitation
254 dissolves carbonate rocks progressively, with leaching resulting in top-soil acidification (Gigon
255 and Rorison, 1972; Partel 2002).

256 The positive relationship between calcareous bedrock and the diversity indexes
257 indicates that their weakly acidic soils can host a greater number of plant species, which,
258 according to J' , were also more equally distributed in terms of their percentage cover. This
259 relationship has never been demonstrated on acidic to weakly acidic *N. stricta*-dominated
260 grasslands, although several studies assessed higher species richness in vegetation communities
261 with higher soil pH (Michalet et al. 2002; Marini et al. 2008). The higher number of plant
262 species, H' , and number of indicator species in the *N. stricta* communities located on calcareous
263 bedrock with respect to those on siliceous one may be related to the species pool effect (Zobel et
264 al. 1998). Indeed, acidophilous species suffered more repeated extinction, by absence of refugia,
265 than calcicole species (Ewald 2003) as during the Quaternary period calcareous substrates were
266 widely available over large areas and for a long time, resulting in the adaptation of many species
267 to higher pH soils (Partel 2002). Furthermore, grasslands on calcareous bedrock are probably
268 also characterised by a larger number of microhabitats (Körner 2003) and can host a high
269 number of plant species with different ecological needs due to their wider ecological spectrum.
270 Indeed, under these conditions, a mosaic of calcareous rocks and acidified soil patches
271 frequently occurs, resulting in a co-occurrence of different soil conditions at various spatial

272 scales, able to support the co-existence of both calcicole and acidophilous plant species (Legros
273 et al. 1987). Some calcicole species, such as *Onobrychis montana* DC. and *Helictotrichon*
274 *sedanense* (Clarion) Holub, can also occur together with acidophilous plant species in sites
275 where the most superficial layers of the soil have been leached and acidified, as their deep root
276 systems allow them to reach the calcareous substrata located in the subsoil (Landolt et al. 2010).
277 Therefore, although the proportion of acidophilous plant species (i.e. species with the
278 phytosociological optimum within the *J. trifidi* and *N. strictae* classes) between calcareous and
279 siliceous bedrock samples was similar, the proportion of calcicole plant species was higher in
280 samples on calcareous bedrock. Another possible factor likely to affect the vegetation
281 composition of species-rich *Nardus* grasslands on calcareous substrates is the presence of loess
282 deposits in the soil, as suggested by Béguin and Pochon (1971) for the Jura Mountains.
283 However, to our knowledge, no specific data on the presence of loess deposits are available for
284 Piedmont alpine region. For this reason, we would advise additional research on the soil features
285 of *N. stricta* grasslands.

286

287 **Conclusions**

288

289 Even though the European Habitat Directive (92/43/EEC) defines as ‘species-rich’ the *N. stricta*
290 communities on siliceous substrates, we highlighted that the *N. stricta* communities on
291 calcareous bedrock, with acidic-to-neutral substrates where calcium has been leached in the top
292 soil, host a higher vascular plant diversity compared to those on the siliceous one. Based on our
293 results, we suggest that conservation actions should primarily focus on *N. stricta* habitats on
294 calcareous substrates for the higher vascular plant diversity they host and to change the title of
295 habitat 6230* ‘Species-rich *Nardus* grasslands, on siliceous substrates in mountain areas (and
296 submountain areas, in continental Europe)’ to take communities of calcareous substrates into
297 consideration.

298 **Disclosure statement**

299 No potential conflict of interest was reported by the authors.

300

301 **Acknowledgements**

302 The authors particularly thank Prof. Andrea Cavallero for his passion and long-term studies on

303 alpine grassland biodiversity and conservation. Special thanks are extended to Paolo Aceto,

304 Marco Brachet-Contol, Davide Cugno, Barbara Martinasso, Chiara Tagliatori, and to all the

305 people who helped carrying out the fieldwork.

306

307 **Funding**

308 Research was carried out under the “Pasture types of Piedmontese Alps” project (Principal

309 Investigator prof. Andrea Cavallero) funded by Regione Piemonte.

310

311 **References**

312

313 Aeschimann D, Lauber K, Martin Moser D, Theurillat JD. 2004. Flora alpina. Bologna (Italy):
314 Zanichelli.

315 Argenti G, Lombardi G . 2012. The pasture-type approach for mountain pasture description and
316 management. *Italian Journal of Agronomy* 7:e39 293–299.

317 Béguin C., Pochon M. 1971. Contribution à l'étude pétrographique et géochimique des sols des
318 nardaies jurassiennes Nardetum jurassicum. *Bulletin de la Société neuchâteloise des*
319 *sciences naturelles* 94:67-76.

320 Bensettiti F, Boulet V, Chavaudret-Laborie C, Deniaud J. 2005. Cahiers d'habitats Natura
321 2000. Connaissance et gestion des habitats et des espèces d'intérêt communautaire. Tome
322 4 - Habitats agropastoraux. MEDD/MAAPAR/MNHN. Paris (France): Éd. La
323 Documentation française.

324 Biancotti A, Bellardone G, Bovo S, Cagnazzi B, Giacomelli L, Marchisio C. 1998.
325 Distribuzione regionale di piogge e temperature. Collana di studi climatologici in
326 Piemonte. Vol. I. Torino (Italy): Cima Icam.

327 Biondi E, Blasi C, Burrascano S, Casavecchia S, Copiz R, Del Vico E, Galdenzi D, Gigante D,
328 Lasen C, Spampinato G, Venanzoni R, Zivkovic L. 2009. Manuale Italiano di
329 interpretazione degli habitat della Direttiva 92/43/CEE. Società Botanica Italiana e
330 Ministero dell'Ambiente e della tutela del Territorio e del Mare, D.P.N. Available online
331 at <http://vnr.unipg.it/habitat/> (accessed 30 January 2017).

332 Biondi E, Burrascano S, Casavecchia S, Copiz R, Del Vico E, Galdenzi D, Gigante D, Lasen C,
333 Spampinato G, Venanzoni R, Zivkovic L, Blasi C. 2012. Diagnosis and syntaxonomic
334 interpretation of Annex I Habitats (Dir. 92/43/EEC) in Italy at the alliance level. *Plant*
335 *Sociology* 49:5–37. doi:10.7338/pls2012491/01.

336 Cavallero A, Aceto P, Gorlier A, Lombardi G, Lonati M, Martinasso B, Tagliatori C. 2007. I
337 tipi pastorali delle Alpi piemontesi. Bologna (Italy): Alberto Perdisa Editore.

338 Chadwick MJ. 1960. *Nardus stricta* L. *Journal of Ecology* 48:255–267.

339 Chang C, Lee P, Bai M, Lin T. 2004. Predicting the geographical distribution of plant
340 communities in complex terrain—a case study in Fushian Experimental Forest, northeastern
341 Taiwan. *Ecography* 27:577–588. doi:10.1111/j.0906-7590.2004.03852.x.

342 Cribari-Neto F, Zeileis A. 2010. Beta Regression in R. *Journal of Statistical Software* 34(2):1–
343 24.

344 Daget P, Poissonet J. 1971. Une methode d’analyse phytologique des Prairies. *Annales*
345 *Agronomiques* 22:5–41.

346 De Cáceres M, Legendre NDP. 2009. Associations between species and groups of sites: indices
347 and statistical inference. *Ecology* 90:3566–3574. doi:10.1890/08-1823.1.Dufrêne M,
348 Legendre P. 1997. Species assemblages and indicator species: The need for a flexible
349 asymmetrical approach. *Ecological Monograph* 67:345–366. doi:10.2307/2963459.

350 Ellenberg H. 2009. *Vegetation Ecology of Central Europe*. 4th ed. Cambridge (United
351 Kingdom): Cambridge.

352 Ewald J. 2003. The calcareous riddle: Why are there so many calciphilous species in the Central
353 European flora? *Folia Geobotanica* 38:357–366. doi:10.1007/BF02803244.

354 Fournier DA, Skaug HJ, Ancheta J, Ianneli J, Magnusson A, Maunder MN, Nielsen A, Sibert J.
355 2012. AD Model Builder: using automatic differentiation for statistical inference of highly
356 parameterized complex nonlinear models. *Optimization Methods and Software* 27:233–
357 249. doi:10.1080/10556788.2011.597854.

358 Galvánek D, Janák M. 2008. Management of Natura 2000 habitats. 6230 *Species-rich *Nardus*
359 grasslands. European Commission.

360 *Gennai M, Foggi B, Viciani D, Carbognani M, Tomaselli M. 2014. The Nardus-rich*
361 *communities in the northern Apennines (N-Italy): A phytosociological, ecological and*
362 *phytogeographical study. Phytocoenologia* 44:55–85. doi:10.1127/0340-269X/2014/0044-
363 0574.

364 Gigon AA, Rorison IH. 1972. The Response of some ecologically distinct plant species to

365 Nitrate- and to Ammonium-Nitrogen. *Journal of Ecology* 60:93–102.

366 Illyés E, Chytrý M, Botta-Dukát Z, Jandt U, Škodová I, Janišová M, Willner W, Hájek O. 2007.

367 Semi dry grasslands along a climatic gradient across Central Europe: Vegetation

368 classification with validation. *Journal of Vegetation Science* 18(6):835–846.

369 Körner C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. 2nd

370 ed. Berlin (Germany): Springer.

371 Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli F, Lämmler W, Nobis M, Rudmann-Maurer

372 K, Schweingruber FH, Theurillat JP, Urmi E, Vust M, Wohlgemuth T. 2010. *Flora*

373 *indicativa: Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz*

374 *und der Alpen*. Bern; Stuttgart; Wien: Haupt Verlag Ag.

375 Legros JP, Party JP, Dorioz JM. 1987. Repartition des milieux calcaires, calciques et acidifiés

376 en haute montagne calcaire humide. *Documents de cartographie écologique*. 30:137-157.

377 Lüth C, Tasser E, Niedrist G, Dalla Via J, Tappeiner U. 2011. Classification of the *Sieversio*

378 *montanae-Nardetum strictae* in a cross-section of the Eastern Alps. *Plant Ecology*

379 212:105–126. doi:10.1007/s11258-010-9807-9.

380 Marini L, Prosser F, Klimek S, Marrs RH. 2008. Water-energy, land-cover and heterogeneity

381 drivers of the distribution of plant species richness in a mountain region of the European

382 Alps. *Journal of Biogeography* 35: 1826–1839. doi:10.1111/j.1365-2699.2008.01924.x.

383 Michalet R, Gandoy C, Joud D, Pages JP, Choler P. 2002. Plant community composition and

384 biomass on calcareous and siliceous substrates in the northern French Alps: comparative

385 effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research* 34:102–

386 113.

387 Moser D, Dullinger S, Englisch T, Niklfeld H, Plutzer C, Sauberer N, Zechmeister HG,

388 Grabherr G. 2005. Environmental determinants of vascular plant species richness in the

389 Austrian Alps. *Journal of Biogeography* 32(7):1117–1127.

390 Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C. 2008. Scale effects and human impact on

391 the elevational species richness gradients. *Nature* 453(7192):216–219.

392 Orlandi S, Probo M, Sitzia T, Trentanovi G, Garbarino M, Lombardi G, Lonati M. 2016.
393 Environmental and land use determinants of grassland patch diversity in the western and
394 eastern Alps under agro-pastoral abandonment. *Biodiversity and Conservation* 25:275–
395 293. doi:10.1007/s10531-016-1046-5.

396 Ozenda P. 1985. *La Vegetation de la Chaîne Alpine dans l’Espace Montagnard Européen*. Paris
397 (France): Masson.

398 Pärtel M. 2002. Local plant diversity patterns and evolutionary history at the regional scale.
399 *Ecology* 83:2361–2366.

400 Pielou EC. 1975. *Ecological diversity*. New York (NY): Wiley.

401 Piemonte C. S. I. (2005). Digital terrain models from CTR 1:10 000 (resolution 50 m).
402 Available at: www.sistemapiemonte.it

403 Pignatti S. 1982. *Flora d’Italia*. Bologna (Italy): Edagricole.

404 Pittarello M, Probo M, Lonati M, Lombardi G. 2016. Restoration of sub-alpine shrub-
405 encroached grasslands through pastoral practices: Effects on vegetation structure and
406 botanical composition. *Applied Vegetation Science* 19:381–390. doi:10.1111/avsc.12222.

407 Ravetto Enri S, Renna M, Probo M, Lussiana C, Battaglini LM, Lonati M, Lombardi G. 2017.
408 Relationships between botanical and chemical composition of forages: a multivariate
409 approach to grasslands in the Western Italian Alps. *Journal of the Science of Food and*
410 *Agriculture* 97(4):1252–1259. doi:10.1002/jsfa.7858.

411 Regione Piemonte. 2006. *Carta numerica delle unità litologiche*. CSI Piemonte, Direzione
412 servizi territorio e ambiente.

413 Scrucca L. 2004. qcc: an R package for quality control charting and statistical process control. *R*
414 *news* 4:11–17.

415 Sebastià M-T. 2004. Role of topography and soils in grassland structuring at the landscape and
416 community scales. *Basic and Applied Ecology* 5:331–346.
417 doi:10.1016/j.baae.2003.10.001.

418 Šmilauer P, Lepš J. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge

419 (United Kingdom): Cambridge University Press.

420 Stanová V, Valachovič M. 2002. Katalóg biotopov Slovenska. DAPHNE-Inš. ed. Bratislava.

421 ter Braak CJF, Smilauer P. 2012. Canoco reference manual and user's guide: software for
422 ordination, version 5.0. Ithaca (USA): Microcomputer Power.

423 Vacchiano G, Meloni F, Ferrarato M, Freppaz M, Chiaretta G, Motta R, Lonati M. 2016.
424 Frequent coppicing deteriorates the conservation status of black alder forests in the Po
425 plain (northern Italy). *Forest Ecology and Management*. 382:31–38.
426 doi:10.1016/j.foreco.2016.10.009

427 Wildi O., Podani J. 2016. Why mean indicator values are not biased. *Journal of Vegetation
428 Science* 27:40–49. doi:10.1111/jvs.12336

429 Wohlgemuth T. 2002. Alpine plant species richness in the Swiss Alps: diversity hot spots
430 reconsidered. *Mémoires Société Bot. Genève* 3:63–74.

431 Wohlgemuth T. 1998. Modeling floristic species richness on a regional scale: A case study in
432 Switzerland. *Biodiversity and Conservation* 7:159–177.

433 Zobel M, Van Der Maarel E, Dupré C. 1998. Species pool: the concept, its determination and
434 significance for community restoration. *Applied Vegetation Science* 1:55–66.
435 doi:10.2307/1479085.

436 Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. *Mixed Effects Models and
437 Extensions in Ecology with R*. New York (NY): Springer.

438

439 **Appendix**

440 Indicator species analysis for *Nardus* grasslands belonging to habitat 6230* located on siliceous
441 and calcareous bedrocks within the Piedmont region. The Indicator value is given for each
442 species together with its significance after 999 permutations (* = $P < 0.05$, ** = $P < 0.01$, *** =
443 $P < 0.001$). Specificity and fidelity values as well as the phytosociological optimum class of
444 each species are presented.

445

446 **Tables**

447

448 **Table 1.** Minimum, maximum, mean values \pm standard deviation of mean (SD), and coefficient449 of variation (CV%) of the biodiversity indexes and environmental variables within *Nardus*

450 grasslands belonging to habitat 6230* of the Piedmont region, north-western Italy.

451

	min	max	mean	\pm SD	CV%
Biodiversity indexes					
Shannon diversity index (H')	0.9	5.1	3.6	\pm 0.68	18.62
Species richness	9.0	64.0	33.9	\pm 11.81	34.84
Pielou's equitability index (J')	0.26	0.90	0.73	0.10	13.70
Topographic variables					
Elevation (m)	1035.0	2229.0	1833.9	\pm 250.56	13.66
Slope (%)	0.7	95.8	34.2	\pm 16.38	47.89
Southness (°)	0.6	180.0	113.2	\pm 45.47	40.18
Climatic variables					
Precipitation (mm)	762.9	2298.4	1338.9	\pm 291.81	21.79
Gams' continentality index	27.8	70.2	53.9	\pm 8.20	15.21
Landolt value for soil reaction (R)	1.3	3.0	2.1	\pm 0.29	13.50

452

453 **Table 2.** Results of Generalised Linear Models (GLMs) showing the effects of topographic
 454 (elevation, slope, southness), climatic variables (total annual precipitation) and bedrock type on
 455 species richness, Shannon diversity (H'), and Pielou's equitability (J') indexes of *Nardus*
 456 grasslands belonging to habitat 6230* of Piedmont region.

457
 458

	Species richness			H'			J'		
	Stand. β^1	SE ²	<i>P</i> -value	Stand. β	SE	<i>P</i> -value	Stand. β	SE	<i>P</i> -value
Intercept	3.44	0.02	*** ³	1.26	0.01	***	0.95	0.02	***
Elevation	-0.10	0.02	***	-0.04	0.01	***	-0.01	0.02	n.s.
Slope	0.07	0.01	***	0.03	0.01	***	0.04	0.02	*
Southness	-0.01	0.01	n.s. ⁴	-0.01	0.01	n.s.	-0.03	0.02	n.s.
Total annual precipitation	-0.19	0.02	***	-0.09	0.01	***	-0.10	0.02	***
Calcareous bedrock ⁵	0.17	0.03	***	0.08	0.02	***	0.09	0.04	*

¹Stand β indicates that each coefficient of the variables (β) has been standardized

²SE is of standardized coefficients (β).

³* = $P < 0.05$; *** = $P < 0.001$

⁴n.s. not significant

⁵Siliceous bedrock was used as the reference category

459

460
 461 **Table 3.** Mean values and SE for species richness, Shannon diversity index (H'), and Pielou's
 462 equitability index (J') of *Nardus* grasslands belonging to habitat 6230* on siliceous and
 463 calcareous bedrocks (Mann-Whitney U-test).

464

	Siliceous bedrock		Calcareous bedrock		<i>P</i>-value
	mean	\pm SE	mean	\pm SE	
Species richness	31.4	\pm 0.57	38.4	\pm 0.84	***
H'	3.5	\pm 0.04	3.9	\pm 0.04	***
J'	0.72	0.005	0.75	0.006	***

*** $P < 0.001$

465

466 **Table 4.** Proportion (in bold type) and number (within brackets) of indicator plant species
 467 having the phytosociological optimum within acidic (*Juncetea trifidi* and *Nardetea strictae*
 468 classes) and calcicole swards (*Elyno-Seslerietea varia*e class) with the results of the χ^2 -test on a
 469 contingency table.

470

	Siliceous bedrock	Calcareous bedrock	χ^2	P-value
Acidic swards				
<i>Juncetea trifidi</i>	14.7 % (5/34)	20.2 % (18/89)	0.2	n.s.
<i>Nardetea strictae</i>	11.8 % (4/34)	7.9 % (7/89)	0.11	n.s.
Calcicole swards				
<i>Elyno-Seslerietea varia</i> e	0.0 % (0/34)	27 % (24/89)	10.03	***

n.s. = not significant; *** = P < 0.001

471