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

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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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16 Marco Pittarello, Michele Lonati, Alessandra Gorlier, Massimiliano Probo[*] and Giampiero

17 Lombardi

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19 *Department of Agricultural, Forest and Food Sciences, University of Torino, Grugliasco, Italy*

20 *Corresponding author. E-mail: massimiliano.probo@unito.it;

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Abstract

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

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

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

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

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

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

Introduction

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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 km^2 within Natura 2000 sites in 24 countries

56 (Galvánek and Janák 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 (Galvánek and Janák 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 (Galvánek and Janák 2008; Ellenberg 2009; Biondi et al. 2012). Such conditions have been

72 reported in Austria (Lüth et al. 2011), France (Bensettiti et al. 2005), Slovakia (Stanová and

73 Valachovič 2002), Spain (Sebastià 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-m^2 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).
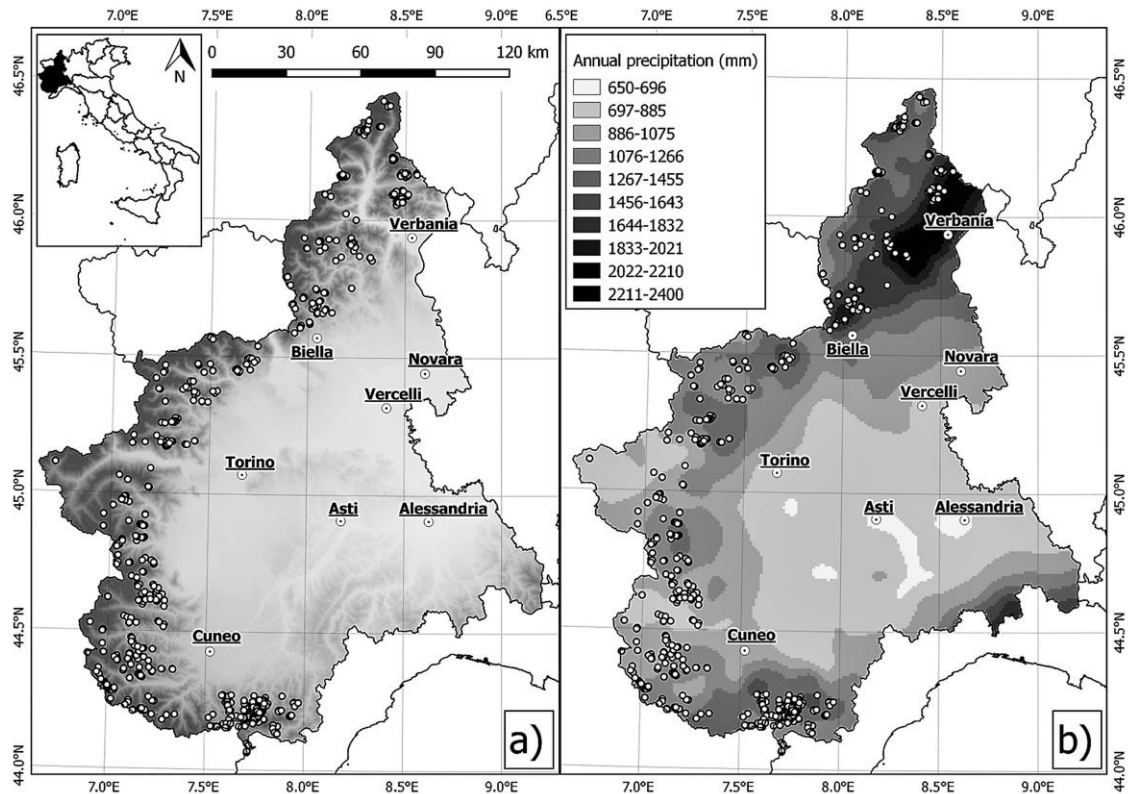
Figure 1. (a) Distribution of *Nardus* grasslands belonging to habitat 6230* in the Alpine chain of Piedmont region (represented on Digital Terrain Model). (b) Mean total annual precipitation map of Piedmont region.

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

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

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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 (southness = 180 - |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   Smilauer 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'

8

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 variae*) were assessed with a χ^2-test on a contingency table.

187

188 **Results**

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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 pyrenaeus* L.) and *Elyno-*

204 *Seslerietea variae* (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).

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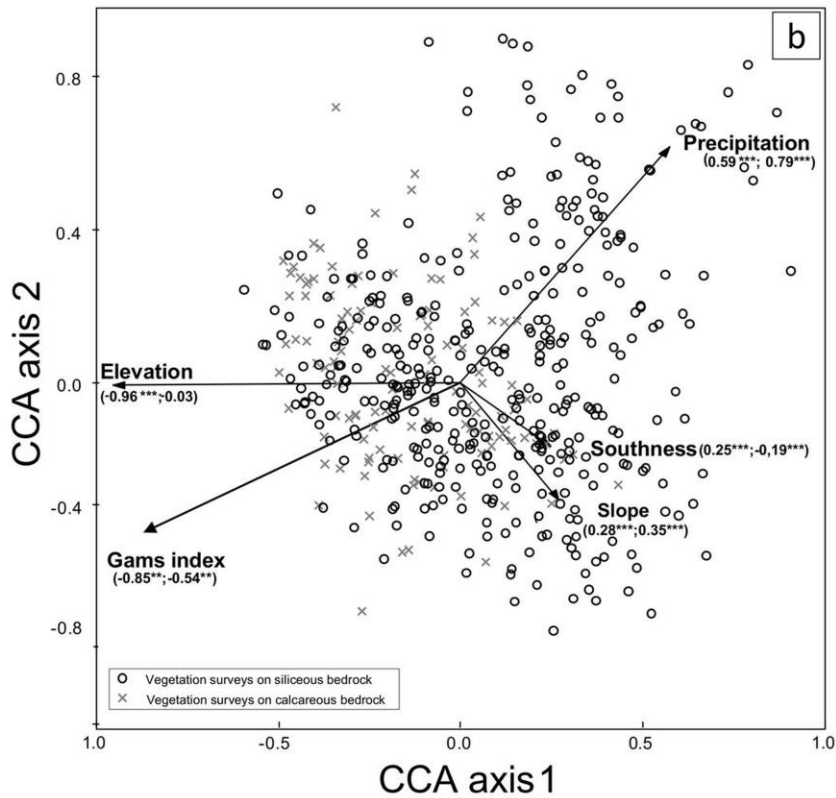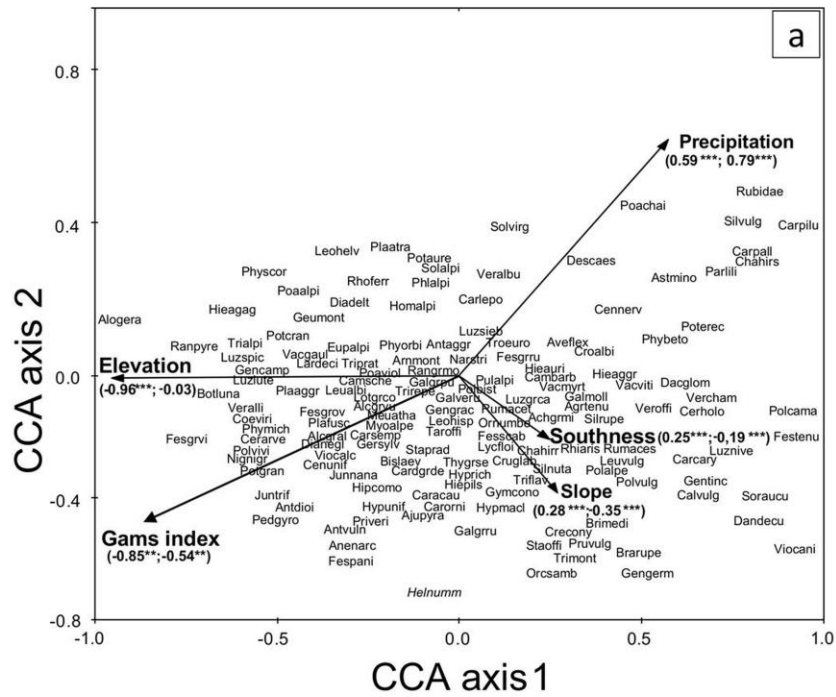
Figure 2. (a) species-environmental variable biplot ordination diagram of the Canonical

Correspondence Analysis (CCA). Only species occurring in more than 5% of 579 vegetation

surveys are represented. Species codes and their attribution to the phytosociological optimal

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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

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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 *sedenense* (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**

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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.

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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 ± standard deviation of mean (SD), and coefficient

449   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	± SD	CV%
Biodiversity indexes					
Shannon diversity index (H')	0.9	5.1	3.6	± 0.68	18.62
Species richness	9.0	64.0	33.9	± 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	± 250.56	13.66
Slope (%)	0.7	95.8	34.2	± 16.38	47.89
Southness (°)	0.6	180.0	113.2	± 45.47	40.18
Climatic variables					
Precipitation (mm)	762.9	2298.4	1338.9	± 291.81	21.79
Gams' continentality index	27.8	70.2	53.9	± 8.20	15.21
Landolt value for soil reaction (R)	1.3	3.0	2.1	± 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]	*P*-value	Stand. β	SE	*P*-value	Stand. β	SE	*P*-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	*

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

[2]SE is of standardized coefficients (β).

[3]* = $P < 0.05$; *** = $P < 0.001$

[4]n.s. not significant

[5]Siliceous 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			*P*-value
	mean	±	SE	mean	±	SE	
Species richness	31.4	±	0.57	38.4	±	0.84	***
H'	3.5	±	0.04	3.9	±	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 variae* 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				
Juncetea trifidi	**14.7 %** (5/34)	**20.2 %** (18/89)	0.2	n.s.
Nardetea strictae	**11.8 %** (4/34)	**7.9 %** (7/89)	0.11	n.s.
Calcicole swards				
Elyno-Seslerietea variae	**0.0 %** (0/34)	**27 %** (24/89)	10.03	***

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

471