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11 **Plant diversity and pastoral value in alpine pastures are maximized at different**
12 **nutrient indicator values**

13

14 *Marco Pittarello^{1,*}, Michele Lonati¹, Alessandra Gorlier¹, Elisa Perotti¹, Massimiliano Probo¹,*
15 *and Giampiero Lombardi¹*

16 ¹Department of Agricultural, Forest and Food Sciences, University of Torino, Largo Braccini 2,
17 Grugliasco, I 10095, Italy;

18 *Corresponding author. E-mail address: marco.pittarello@unito.it

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21 **Abstract**

22 In alpine environments, very low and very high amounts of soil nutrients are generally
23 associated to the lowest plant diversity and forage quality levels. Both soil nutrient content and
24 forage quality and productivity of a site can be inferred from plant species lists, by attributing
25 each species a nutrient indicator value (N value) and a quality value, and computing
26 respectively average N Value and Pastoral Value (PV) at site scale. We used a wide dataset of
27 vegetation surveys carried out in the pastures of Western Italian Alps to 1) evaluate if N values,
28 PV, and plant diversity (species richness and Shannon diversity index) change along an
29 elevation gradient, from montane/sub-alpine pastures (i.e. the ones located below treeline) to
30 alpine pastures (above treeline), 2) analyze the relationships between N value and plant diversity
31 indexes and between N value and PV, and 3) evaluate whether the N values associated to the
32 highest plant diversity and PV differ.

33 Plant diversity, PV, and N values were higher in the pastures located at lower elevation. Plant
34 diversity and PV showed a unimodal relation with N values, both in the montane/sub-alpine and
35 alpine belts. Plant diversity indexes peaked at intermediate N indicator values, confirming the
36 Intermediate Disturbance Hypothesis, while PV peaked at higher N values, where higher
37 nutrient availability in the soil increased plant species productivity, growth rate, leaf turnover
38 and nutrient concentration, digestibility, and palatability. The overall shape of the curves as well
39 as the N values at which plant diversity and PV values peaked did not considerably change from
40 montane/sub-alpine to alpine pastures. These results suggest that an extensive pastoral
41 management is recommended when plant diversity conservation is the main goal. Conversely, a
42 more intensive management can produce an overall enhancement of forage quality/productivity
43 of alpine pastures, but only if restricted under certain critical N values.

44

45 **Keywords.** Biodiversity conservation, Forage quality, Generalized Additive Models (GAM),
46 Grazing management, Hump-shaped curves, Landolt indicator values

47 **Abbreviations.** PV = Pastoral Value, N Landolt = Landolt indicator value for soil nutrient
48 content (N), H' = Shannon diversity Index

49 **Nomenclature.** Pignatti 1982

50

51 **1. Introduction**

52 Pastoral management is one of the most important drivers of soil and plant nutrient
53 concentration in alpine pastures, due to the removal and accumulation of nutrients that livestock
54 exert by grazing and depositing dung and urine, respectively (Jewell et al., 2007; Lonati et al.,
55 2015). The concentration of soil nutrients, mainly nitrogen and phosphorous, affects plant
56 diversity and forage yield and quality as well (Güsewell et al., 2012; Gardarin et al., 2014). In
57 alpine environments, very low and very high amounts of soil nutrients are generally associated
58 to the lowest plant diversity and forage quality levels; low amounts of nutrients favor the
59 dominance of few oligotrophic plant species in the sward, whereas very high amounts promote
60 the dominance by a few nitrophilous plants. In both cases, these plant species are generally
61 characterized by low nutritive value or high levels of toxic compounds (Aerts and Chapin, 1999;
62 Iussig et al., 2015; Orlandi et al., 2016). For these reasons, identifying and maintaining adequate
63 levels of nutrient concentration in the soil is a major management goal when targeting plant
64 diversity conservation and forage yield and quality.

65 Soil nutrient content can be measured directly by chemical analyses or through
66 vegetation-derived ecological indicators, such as nutrient (N) indicator values, which have the
67 advantage to be cost-effective, since they are calculated from plant species lists (Hintermann et
68 al., 2000). The N indicator values were originally proposed by Ellenberg (1974) for Central
69 Europe and by Landolt (1977) for Swiss flora. Recently, they have been updated and extended
70 to whole alpine flora by Landolt et al. (2010), so that they are now available for each plant
71 species growing in the Alps. Such indicator values rely on the knowledge and extensive field
72 experience of botanists and ecologists, so to correctly characterize the condition of a site by
73 means of ecological indicator values, a consideration of as many as possible plant species
74 growing at that site is recommended (Landolt et al., 2010). The N indicator values can properly
75 characterize an area (Tölgyesi et al., 2014) and they are well correlated to the supply of several
76 nutrients (e.g. nitrogen, phosphorous, and potassium) and to the potential biomass production of
77 the site (Diekmann, 2003). For these reasons, their application has strongly increased in the
78 literature since year 2000 (Wildi, 2016).

79 Another synthetic index derived from vegetation surveys is the Pastoral Value (PV),
80 which summarizes forage yield, quality, and palatability for livestock (Daget and Poissonet,
81 1969). Since it is calculated from sward botanical composition, the PV is more constant and less
82 influenced by temporal fluctuations than other forage parameters, such as aboveground biomass,
83 organic matter digestibility, or crude protein content (Daget and Poissonet, 1969). Therefore,
84 especially in pastures characterized by a high cover of perennial species, it can provide a
85 reliable estimate of the grassland carrying capacity, which has been defined by Allen et al.
86 (2011) as the maximum livestock stocking rate achieving a target level of animal performance,

87 in a specified grazing system, that can be applied over a defined time without deterioration of
88 the grazing land. The average annual carrying capacity of a particular alpine grassland can thus
89 be calculated by multiplying its grazable area with PV and with altitudinal and slope
90 coefficients, as defined by Cavallero et al. (2007). Moreover, the PV is directly related to forage
91 energy and alpha-linolenic acid content (Daget and Poissonet, 1969; Ravetto Enri et al., 2017).
92 Because of its reliability and simplicity of computation, PV has been widely used, e.g. in south-
93 western Alps, (Probo et al., 2014, 2016; Pittarello et al., 2016a), in the Apennines (Cervasio et
94 al., 2016), in Sardinia (Bagella et al., 2013; Bagella et al., 2017), in southern Italy (Fracchiolla
95 et al., 2017), in central and eastern Pyrenees (Sebastià et al., 2008), in Romania (Sărățeanu and
96 Alexandru, 2011), and in central Chile (Ovalle et al., 1999).

97 In mountain ecosystems a general decrease in plant diversity, N indicator, and forage
98 values occur with increasing elevation, due to differences in growing season, temperature,
99 precipitation, bedrock type, soil, nutrient contents, deposition, and mineralization rates (Körner,
100 2003; Güsewell et al., 2012). In this study we used a wide dataset of vegetation surveys carried
101 out in the pastures of the Western Italian Alps to: 1) evaluate if N indicator, PV, and plant
102 diversity indexes (species richness and Shannon diversity) change along an elevation gradient,
103 from montane/sub-alpine pastures (i.e. the ones located below treeline) to alpine pastures (i.e.
104 the ones located above treeline), 2) analyze the relationships between N value and plant
105 diversity indexes and N value and PV, and 3) evaluate whether the N values associated to the
106 highest plant diversity and PV differ.

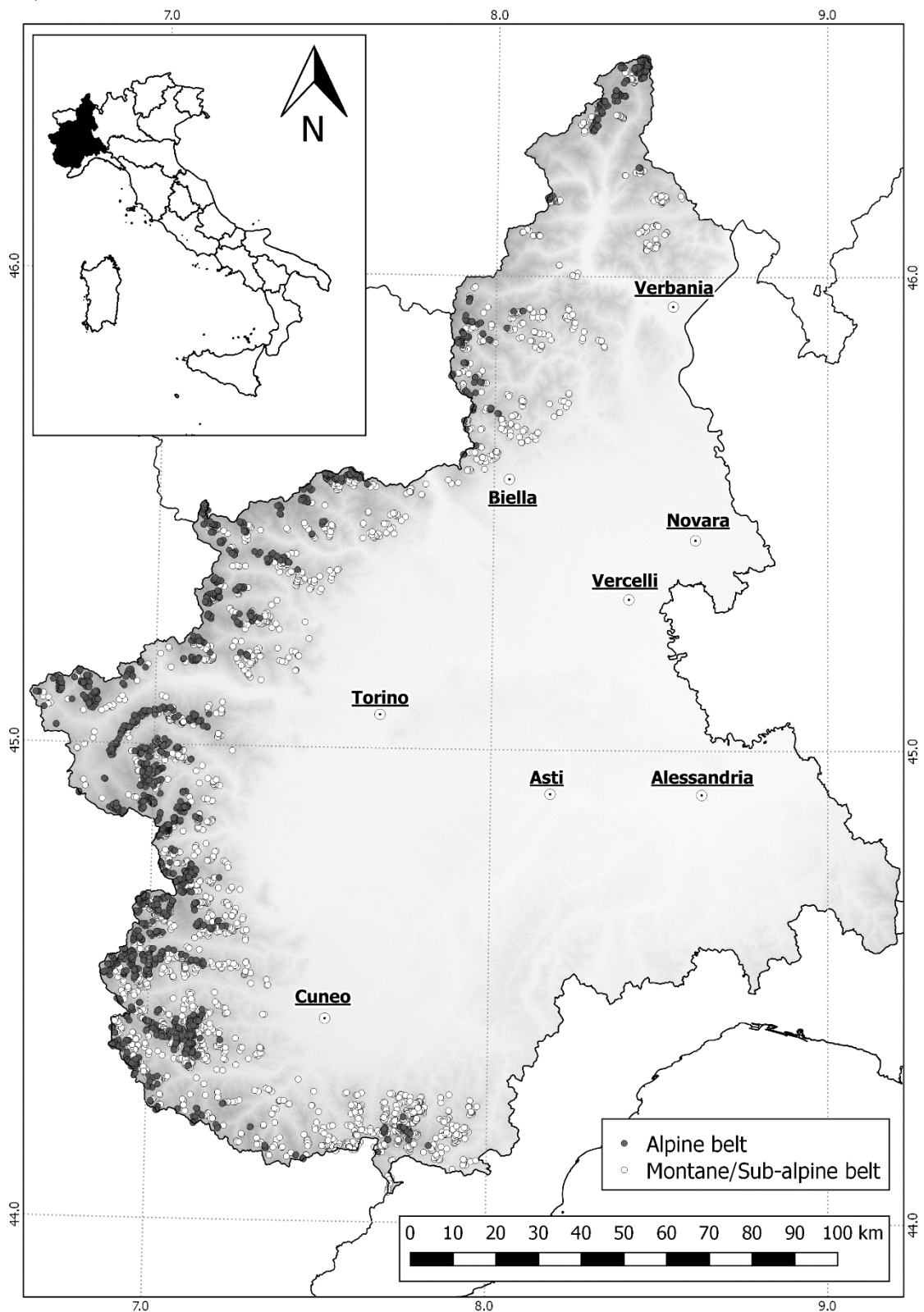
107 **2. Materials and Methods**

108 2.1. Study area and vegetation surveys

109 Data were collected across the Western Italian Alps of Piedmont Region during the
110 period 2001 – 2007. In that period, 3839 surveys were carried out to characterize the vegetation
111 composition of alpine pastures, which are mainly grazed by domestic livestock during
112 summertime (Cavallero et al., 2007) (Figure 1).

113

114 **Figure 1.** Distribution of 3839 vegetation surveys in the Western Italian Alps, represented on
115 Digital Terrain Model. White circles represent the vegetation surveys located below the treeline
116 (i.e. in the montane and sub-alpine belts), dark circles the ones located above (i.e. in the alpine
117 belt).



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120 Elevation ranged from 491 to 2901 m a.s.l.. Vegetation surveys were carried out within
121 vegetation communities developed over a wide spectrum of soil nutrient content conditions as
122 described in Cavallero et al. (2007), from oligotrophic (e.g. pastures dominated by *Carex*
123 *sempervirens* Vill., *Nardus stricta* L., *Trifolium alpinum* L. and *Carex sempervirens*, *Festuca*
124 *paniculata* (L.) Sch. et Th., and *Festuca ovina* s.l.) to nitrophilous vegetation communities (e.g.
125 pastures dominated by *Chenopodium bonus-henricus* L., *Rumex alpinus* L., and *Urtica dioica*
126 L.), through mesotrophic (e.g. pastures dominated by *Festuca rubra* s.l. and *Agrostis tenuis*
127 Sbirth. and *Festuca violacea* s.l.) and eutrophic (e.g. pastures dominated by *Alchemilla vulgaris*
128 s.l., *Dactylis glomerata* L., and *Trisetum flavescens* (L.) Beauv.) vegetation communities.

129 Each survey was conducted along a 25-m linear transect in which botanical composition
130 was determined using the vertical point-quadrat method (Daget and Poissonet, 1971). At every
131 50-cm interval along the transect, plant species touching a steel needle were identified and
132 recorded (i.e. a total of 50 measurements). Since occasional species are often missed by this
133 method, a complete list of all other plant species included within a 1-m buffer area around the
134 transect line (vegetation plot) was also recorded (Pittarello et al., 2016b). Plant nomenclature
135 followed Pignatti (1982).

136 The N Landolt indicator value (hereafter ‘N Landolt’; Landolt et al., 2010) was
137 attributed to each plant species recorded in vegetation surveys and to all occasional plant species
138 within vegetation plots. An average N Landolt was calculated afterwards for each survey using
139 species presence/absence data.

140 For each plant species recorded in the vegetation surveys, the frequency of occurrence
141 (f_i = number of occurrences/50 points), which is an estimate of species canopy cover (Probo et
142 al., 2013), was calculated. Species Relative Abundance (SRA_i) was computed at each transect
143 and used to detect the proportion of different species according to the equation of Daget and
144 Poissonet (1971):

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

145 A SRA value = 0.3 was attributed to all occasional plant species found within vegetation plot
146 but not along linear transects (Vacchiano et al., 2016). To estimate PV, we attributed each
147 species an Index of specific quality (ISQ) (Daget and Poissonet, 1971; Cavallero et al., 2007).
148 The ISQ depends on the preference, morphology, structure, and productivity of the plant species
149 and it ranges from 0 (low) to 5 (high) (Daget and Poissonet, 1971). The PV, which ranges from
150 0 to 100, was calculated as follows (Daget and Poissonet, 1971):

$$PV = \sum_{i=1}^n (SRA_i \cdot ISQ_i) \cdot 0.2$$

151 where ISQ_i is the ISQ value for the species i (Cavallero et al., 2007).

152 Plant diversity was expressed in terms of species richness and Shannon diversity index
153 (H'). Shannon diversity index (H') was calculated for each vegetation transect according to the
154 following equation:

$$H' = - \sum_{i=1}^{i=n} \left\{ \frac{SRA_i}{100} \times \log_2 \left(\frac{SRA_i}{100} \right) \right\}$$

155
156 The elevation of each vegetation survey was calculated from a Digital Terrain Model
157 (50-m resolution) (CSI Piemonte 2005). Since the altitudinal limit between montane/sub-alpine
158 and alpine belt can vary linearly with the latitude (Ozenda, 1985), the treeline limit was linearly
159 interpolated from the southern zone (2300 m a.s.l. – 43.5° latitude) up to the northern zone
160 (2000 m a.s.l. – 46.5° latitude) of Piedmont. Elevational and latitudinal limits were set
161 according to Ozenda (1985). Vegetation surveys were attributed to the montane/sub-alpine or
162 alpine belt depending on whether their elevation was lower or higher than the interpolated
163 treeline limit computed for the latitude at which the survey was conducted. According to this
164 method, 2196 vegetation surveys were located below the treeline and 1643 above it (Figure 1).

165 *2.2. Data analysis*

166 Mann-Whitney U-tests (Sokal and Rohlf, 1995) were used to assess whether N Landolt, PV,
167 species richness, and H' differed between montane/sub-alpine and alpine pastures.

168 Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) were
169 performed to analyze the relationships between N Landolt and PV, species richness, and H' .
170 The models were performed separately for the vegetation surveys located in the montane/sub-
171 alpine and alpine belts. The GLMs (Zuur et al., 2009) were fitted by using both the linear and
172 quadratic term of N Landolt to check for non-linear relationships. For the GAMs, a cubic
173 regression spline was used as smoothing function of N Landolt and the cross-validation was
174 applied to estimate the optimal amount of smoothing, expressed as ‘effective degree of freedom’
175 (edf). This is a value ranging between 0 and infinity, and the higher the edf, the more non-linear
176 is the smoothing spline (a GAM with edf = 1 is a straight line). The more complex pattern
177 described by GAMs through non-parametric smoothers may give additional information in the
178 graphical output compared to GLMs, as they allow to capture the shape of a relationship without
179 choosing a specific parametric form (Crawley, 2007). Being PV and H' positive and continuous
180 variables not normally distributed (the normality was tested using the Shapiro-Wilk test), a
181 gamma distribution was used in the models. Since species richness was a count overdispersed
182 variable, a negative binomial distribution was specified (overdispersion in the data was tested by
183 the *qcc* R package; Scrucca, 2004). In case of a possible unimodal relationship, peak values
184 were detected by the first derivative of GLMs.

185 Statistical analyses were performed using the software R 3.2.3 for Windows (R Core Team,
 186 2015). Generalized Linear Models were performed using the “glm” and “glm.nb” functions of
 187 the “stats” package (R Core Team, 2015), whereas GAMs were run using the “gam” function of
 188 the “mgcv” package (Wood, 2011).

189 3. Results

190 A total of 1033 plant species was recorded in the vegetation surveys (the complete list of all
 191 plant species, with their respective N and ISQ values is provided in Appendix A). Mann-
 192 Whitney tests showed significant differences between N Landolt, PV, species richness, and H'
 193 of the pastures located in the montane/sub-alpine belt compared to the alpine belt ones (Table
 194 1).

195

196 **Table 1.** Mean values and Standard Error (SE) for Landolt indicator value for soil nutrient
 197 content (N Landolt), forage pastoral value (PV), species richness, and Shannon diversity index
 198 (H') of montane/sub-alpine and alpine pastures.

	Montane/sub-alpine pastures	Alpine pastures	
	mean ± SE	mean ± SE	<i>P</i> -value
N Landolt	2.5 ± 0.01	2.2 ± 0.01	***
PV	22.5 ± 0.22	18.3 ± 0.18	***
species richness	37.3 ± 0.28	29.4 ± 0.25	***
H'	3.8 ± 0.01	3.6 ± 0.02	***

199 *** $P < 0.001$ (Mann-Whitney U-test)

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202 With both GLMs and GAMs, a unimodal relationship of plant diversity indexes and PV with the
 203 N Landolt was detected, both in the montane/sub-alpine and alpine belts (Figure 2). A hump-
 204 shaped relation emerged due to the significance of the quadratic term in all GLMs (Appendix B)
 205 as well as of the smoothing function of N Landolt and the effective degree of freedom (edf),
 206 which was always greater than 1 in all GAMs (Appendix C). Moreover, the fitted values of both
 207 the GLMs and GAMs widely overlapped (Figure 2). The N Landolt to which each predictor
 208 peaked was similar between montane/sub-alpine and alpine belts: species richness peaked at N
 209 Landolt of 2.5 and 2.2, H' at 2.6 and 2.3, and PV at 3.1 and 3.1, respectively at montane/sub-
 210 alpine belt and at alpine belt.

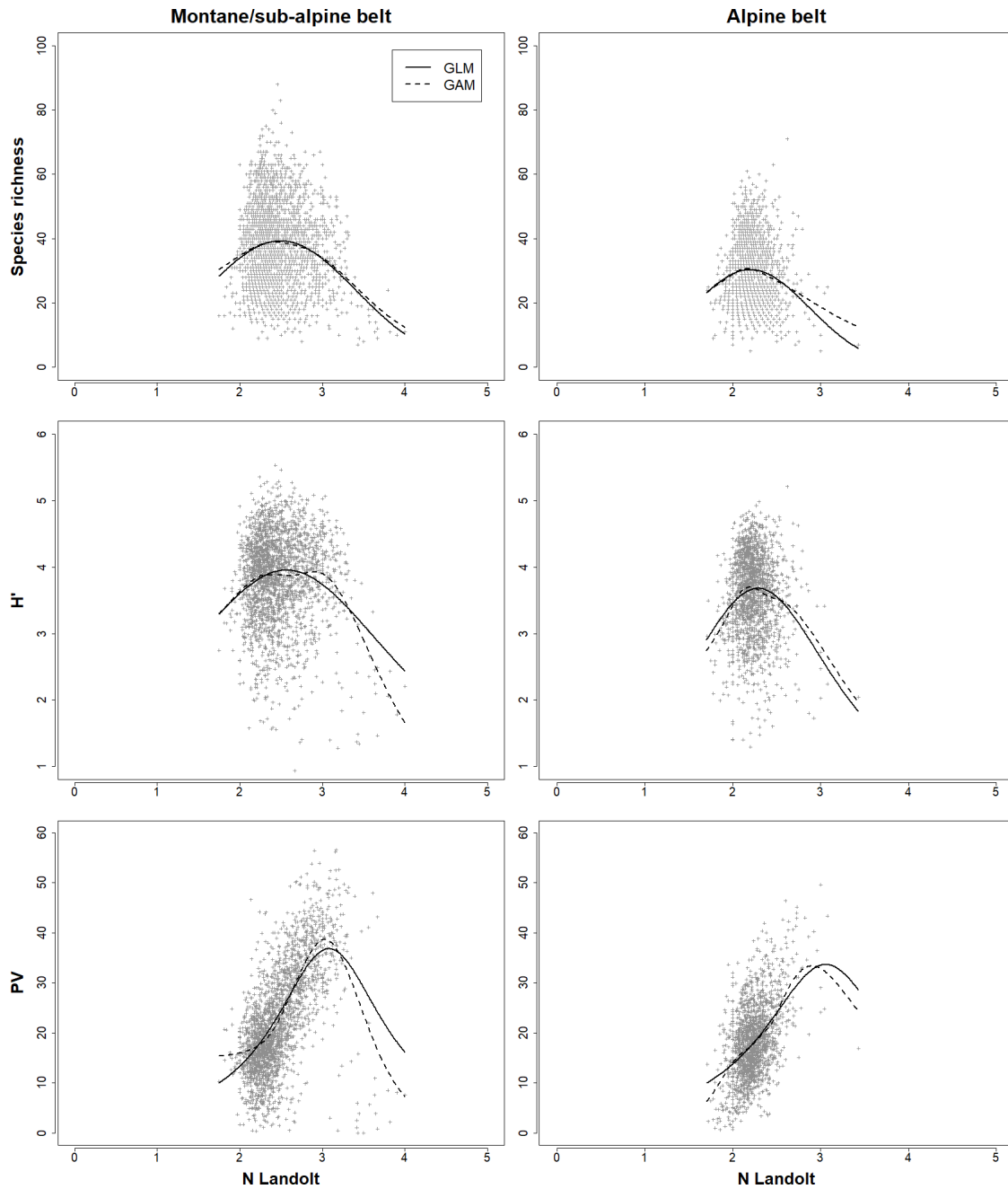
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215 **Figure 2.** Relationships between Landolt indicator value for soil nutrient content (N Landolt)
 216 and species richness, Shannon diversity index (H'), and pastoral value (PV) of montane/sub-
 217 alpine and alpine pastures. The solid lines represent the predicted values by the Generalized
 218 Linear Models (GLM) using both the linear and quadratic term of N Landolt. The dashed lines
 219 represent the predicted values by the Generalized Additive Models (GAM) using a cubic
 220 regression spline as smoothing function of N Landolt and the cross-validation to estimate the
 221 optimal amount of smoothing.
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225 4. Discussion

226 The lower values of plant diversity, pastoral value, and soil nutrient content of alpine
 227 pastures if compared to montane/sub-alpine ones were consistent with the results obtained by

228 other studies (Moser et al., 2005; Güsewell et al., 2012). The number of species functionally
229 adapted to tolerate the stress imposed by extreme pedo-climatic conditions at high elevation
230 (e.g. short growing season, low temperatures, and shallow soils) decreases with increasing
231 altitude (Körner, 2003). Due to such environmental constraints, aboveground biomass is also
232 generally lower than in montane/sub-alpine belts, which results in a lower ISQ of the species
233 found at higher elevation and a lower PV of plant communities. Under these lower productivity
234 conditions, pastures have lower carrying capacity and can be exploited less intensively, i.e. with
235 lower stocking rates. Consequently, weaker organic fertilization by grazing animals and human
236 activities contributes to determine a lower soil nutrient content if compared to montane/sub-
237 alpine belt pastures. Indeed, N Landolt has been considered as a proxy of management intensity
238 (Dietschi et al., 2007; Strebel and Bühler, 2015). The PV measured in these extensively
239 managed alpine pastures was comparable with the PV assessed in other extensive semi-natural
240 grassland ecosystems, such as Mediterranean (Bagella et al., 2013; Bagella et al., 2017;
241 Fracchiolla et al., 2017) and Apennine grasslands (Cervasio et al., 2016). The same authors
242 measured PV up to 60-70 only under more intensive management, i.e. after N and P fertilization
243 (Bagella et al., 2017), ploughing and sowing of forage mixtures (Cervasio et al., 2016), or in
244 permanent grasslands developed over former arable lands, where the contribution of sown
245 legumes was still considerable (Fracchiolla et al., 2017).

246 Even though plant diversity and PV differed between montane/sub-alpine and alpine
247 pastures, all these variables showed a unimodal relationship with N Landolt, both in the
248 montane/sub-alpine and alpine belts. Gusewell et al. (2012) detected a “hump-shaped” curve
249 between species richness and N Landolt only in sub-alpine and alpine grasslands, but they found
250 species richness linearly and negatively related to N Landolt in Swiss lowland and montane
251 grasslands. The different shape of this relationship at lower elevations might result from a
252 narrower range of the different conditions analyzed compared to our study. Indeed, the greater
253 the range in the N value predictors, the more probable is the development of “hump-shape”
254 relationships (Guo and Berry, 1998; Espinar, 2006). Such a response was also assessed by other
255 authors with the direct measurement of soil nitrogen content (Vermeer and Berendse, 1983;
256 Janssens et al., 1998).

257 Species richness and H' peaked at intermediate N Landolt level, while PV peaked at
258 higher N Landolt levels. The highest level of plant diversity at intermediate levels of
259 management intensity was found by several other studies (Olf and Ritchie, 1998; Dupre and
260 Diekmann, 2001; Eek and Zobel, 2001; Dietschi et al., 2007; Orlandi et al., 2016), confirming
261 the Intermediate Disturbance Hypothesis, which states that species richness peaks at
262 intermediate levels of disturbance/management as a result of the co-existence of several species
263 due to ecological niche overlaps (Grime, 1973; Connell, 1978; Marini et al., 2008).

264 In contrast, PV peaked at higher management intensity, where the higher nutrient availability in
265 the soil increased plant species productivity (Mattson, 1980), growth rate, leaf turnover and
266 nutrient concentration, digestibility, and palatability (Aerts, 1999). The PV had low values
267 where the nutrient content in the soils was low, as plant species were characterized by lower
268 ISQ because of tougher leaves with lower concentrations of nutrients, slower turnover rates, and
269 higher concentration of secondary compounds, acting as defense against herbivories (Aerts and
270 Chapin, 1999). A sharp decline in PV was also detected when soil nutrient content exceeded
271 optimal levels, due to the dominance of a low number of nitrophilous species (e.g. *R. alpinus*)
272 within plant communities (Zaller, 2004; Bohner, 2005). These species, which are competitive,
273 fast growing, and highly efficient in the use of both above- and below-ground resources (Aerts,
274 1999; Bohner, 2005; Hejcman et al., 2012; Šilc and Gregori, 2016) are often characterized by
275 prickles (e.g. *Carduus* and *Cirsium*) or high content of irritating (e.g. *U. dioica*) and/or toxic
276 compounds (e.g. *C. bonus-henricus*, *R. alpinus*, *Veratrum album* L.) (Schaffner et al., 2001; Šilc
277 and Gregori, 2016). These morphological and chemical attributes negatively affect their forage
278 quality and palatability, and strongly lower their ISQ and the PV of the communities in which
279 they develop (Roggero et al., 2002; Cavallero et al., 2007). At N Landolt values lower than the
280 peak, i.e. when soil nutrient content was below optimal levels, the reduction in PV was much
281 more pronounced than that in plant diversity. This result can be interpreted considering that
282 some plant species, which were often dominant under nutrient poor conditions and thus
283 characterized by low productivity, forage quality, and palatability (e.g. the mat-grass *Nardus*
284 *stricta* L.), were often found in species-rich communities, such as *N. stricta* grasslands, which
285 are also protected by the European Habitat Directive (92/43/CEE) because of their high plant
286 diversity. Indeed, when nutrient availability in the soil is not sufficient to allow nitrophilous
287 species become dominant, the number of plant species is generally high (Huston, 1979).

288 Interestingly, the overall shape of curves as well as N indicator values at which plant
289 diversity and PV values peaked did not considerably change from montane/sub-alpine to alpine
290 pastures. Consequently, even if different plant communities with diverse ecological needs and
291 functional adaptations occurred along the explored elevation gradient, they showed similar
292 inherent ecological relationships. This result underlines that pastoral management intensity
293 produced similar gradients and responses in plant communities, regardless they were located in
294 the lower or upper alpine belts.

295 **5. Conclusions**

296 Despite plant diversity and PV were lower in alpine than in montane/sub-alpine pastures
297 and plant diversity peaked at lower N Landolt values than PV, they showed similar unimodal
298 relationships with N indicator values along the elevational gradient analyzed. Management

299 implications regarding the identification of specific and sustainable N Landolt thresholds, which
300 are proxies of pastoral management intensity, can be derived from the current study: an
301 intermediate intensity pastoral management, associated to intermediate stocking and fertilization
302 rates, is recommended when biodiversity conservation is the main goal. Conversely, a more
303 intensive management can produce an overall enhancement of forage quality/productivity of
304 alpine pastures, but only if restricted under certain critical N values.
305

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312

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473

474 **8. Appendices**

475 **Appendix B.** Results of Generalized Linear Model (GLM) in which forage Pastoral Value (PV),
 476 species richness, and Shannon diversity index (H') were modeled with the linear term and the
 477 quadratic term of Landolt indicator value for soil nutrient content (N), in the alpine and
 478 montane/sub-alpine belt, respectively.
 479

	Montane/Sub-alpine belt				Alpine belt			
	Estimate	SE	t/z	P-value	Estimate	SE	t/z	P-value
Species richness								
Family: Negative binomial								
Link: Log								
Intercept	0.00	0.387	-0.01	n.s.	-1.84	0.792	-2.32	*
N	2.95	0.298	9.878	***	4.78	0.690	6.921	***
N ²	-0.59	0.057	-10.4	***	-1.09	0.150	-7.23	***
H'								
Family: Gamma								
Link: Log								
Intercept	0.76	0.053	14.23	***	1.37	0.121	11.39	***
N	-0.39	0.041	-9.54	***	-0.96	0.106	-9.14	***
N ²	0.08	0.008	9.686	***	0.21	0.023	9.147	***
PV								
Family: Gamma								
Link: Log								
Intercept	0.41	0.017	24.42	***	0.39	0.038	10.21	***
N	-0.25	0.013	-19.8	***	-0.23	0.031	-7.42	***
N ²	0.04	0.002	17.36	***	0.04	0.006	5.861	***

480 ***: P < 0.001
 481 n.s.: not significant
 482

483 **Appendix C.** Results of Generalized Additive Model (GAM) in which forage Pastoral Value
 484 (PV), species richness, and Shannon diversity index (H') were modeled with a smoothing
 485 function of N Landolt, in the alpine and montane/sub-alpine belt, respectively. A cubic
 486 regression spline was used as smoothing function and the cross-validation was applied to
 487 estimate the optimal amount of smoothing.
 488

	Montane/Sub-alpine belt				Alpine belt			
Species richness								
Family: Negative binomial								
Link: Log								
	Estimate	SE	z	P-value	Estimate	SE	z	P-value
Intercept	3.61	0.022	167.1	***	3.37	0.025	134.6	***
	edf	Ref.df	Chi.sq	P-value	edf	Ref.df	Chi.sq	P-value
s(N)	3.00	3.780	16.46	**	2.69	3.443	9.12	*
H'								
Family: Gamma								
Link: Log								
	Estimate	SE	t	P-value	Estimate	SE	t	P-value
Intercept	1.34	0.004	370.0	***	1.28	0.004	310.5	***
	edf	Ref.df	F	P-value	edf	Ref.df	F	P-value
s(N)	5.295	6.317	27.04	***	5.81	6.106	19.65	***
PV								
Family: Gamma								
Link: Log								
	Estimate	SE	t	P-value	Estimate	SE	t	P-value
Intercept	3.13	0.007	432.7	***	2.89	0.009	319.6	***
	edf	Ref.df	F	P-value	edf	Ref.df	F	P-value
s(N)	5.24	6.263	247.3	***	5.93	6.959	65.41	***

489 ***: $P < 0.001$; **: $0.001 < P < 0.01$