1 **A multifaceted approach for beech forest conservation:**

2 **environmental drivers of understory plant diversity**

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4 Short running title: A multifaceted approach for conservation

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23

24 **Abstract**

25

26 Studies addressing multiple aspects of biodiversity simultaneously (i.e., multifaceted

27 approaches) can quantify plant diversity-environment links comprehensively, however they are

28 scant in forests. This is because of the multidimensional nature of plant diversity. We studied

29 taxonomic, functional and phylogenetic diversity patterns in 19 beech forest understory plots in

30 two areas belonging to a biodiversity monitoring plan in Tuscany, Italy. We performed linear-

31 mixed-effect models to quantify the influence of elevation (proxy for macroclimate), aspect

32 (affecting microclimate), and basal area (related to microclimate and stand maturity) on diversity

33 facets of vascular plants. Elevation played a major role in shaping diversity: high-elevation plots

34 were less rich in species and had a reduced functional diversity of storage organs that may

35 promote cold-tolerance. Conversely, the diversity of flowering phenology increased with

36 elevation, thus low-elevation vegetation converged functionally towards a common, short

37 blooming period. This strategy may be advantageous for understory plants in the deciduous

38 beech forests experiencing longer growing seasons, hence more extended canopy closure at

39 lower elevations. Basal area negatively affected foliar and multiple-trait functional diversity

40 which may be associated with highly selective and competitive environment for light capture in

41 closed canopy, mature stands. Slope aspect did not exert any significant effect on diversity

42 facets, neither did interactions among predictors. Overall, these results confirm the usefulness

43 of implementing multifaceted approaches to i) better understand the influence of environmental

44 drivers on different aspects of plant diversity, and ii) inform the biodiversity monitoring plan that

45 is in place in the study forests by systematically including functional diversity instead of

46 taxonomic metrics only.

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48 *Keywords*: conservation practices; elevation gradient; forest ecology; functional diversity;

49 phylogenetic diversity; species richness

50

1. Introduction

52

53   Climate and management regimes both contribute to determine forest diversity, functioning,

54   and dynamics (Laughlin et al., 2011; Pausas, 2015). Changing climatic conditions can trigger

55   widespread plant responses, and these changes may generate feedback-effects on forest

56   assembly and functioning (Sánchez-Salguero et al., 2017). Also, alteration of management

57   regimes, such as logging frequency, can produce considerable effects on forest biota

58   (Campetella et al., 2016). Management is generally associated with disturbance involving

59   biomass removal and defines stand maturity (Lebrija-Trejos & Bongers, 2008; Lebrija-Trejos et

60   al., 2010; Pinho et al., 2017). Therefore, both changes in climate and disturbance regime can

61   alter forest diversity, composition, and dynamics, such as treeline upward shifts (e.g., Gazol et

62   al., 2017; Vitali et al., 2018).

63   Examining biodiversity patterns is a complex and multidimensional task by nature. Studies

64   that simultaneously consider relations between different diversity metrics capturing different

65   facets of diversity (i.e., taxonomic, functional, phylogenetic indices) and environmental variables

66   can assist along this challenging quest (Cadotte & Tucker, 2018). These multifaceted

67   approaches can therefore greatly advance the understanding about drivers of plant diversity

68   (e.g., Spasojevic & Suding, 2012; Molina-Venegas et al., 2016). Thus far, such approaches

69   have been applied across different ecosystems and regions: alpine tundra (Spasojevic &

70   Suding, 2012), Mediterranean dune (Marcantonio et al., 2014), shrub (Molina-Venegas et al.,

71   2016) and mountain communities (Lopez-Angulo et al., 2018), and tropical forests (Swenson,

72   2011; Kandlikar et al., 2018). To our knowledge, multifaceted studies are scarce in temperate

73   forests (but see Swenson et al., 2017).

74   In Europe, forests dominated by beech (*Fagus sylvatica* L., Fagaceae) are important for

75 wood production, but are also of particular interest for plant ecology, biogeography and

76 conservation (Magri, 2008; Bradshaw et al., 2010; Marcantonio et al. 2013; Jiménez-Alfaro et

77 al., 2018). Within the Mediterranean basin, beech forests found in the Apennines are exposed to

78 warmer, drier climates compared to northern occurrences of this forest type, influencing their

79 composition and dynamics (Scolastri et al., 2017; Vacchiano et al., 2017). Additionally, their

80 persistence can be affected by the spatial isolation from the Central European distribution area

81 that may compromise gene-flow (Magri, 2008; Bradshaw et al., 2010). Also, intensifying land-

82 use changes and climate fluctuations may have large interplaying ecological consequences,

83 such as treeline upward shift in mountains (Gazol et al., 2017; Vitali et al., 2018). Yet, plant

84 diversity-environment links remain still challenging to be quantified. Therefore, more research

85 aiming at disentangling effects caused by climate and management on beech forests diversity is

86 timely.

87   In beech forests, previous research from Apennines investigated species and functional

88 diversity patterns in response to changing management regimes, i.e., species richness

89 decreasing towards older plots, and clonal and bud bank traits tightly linked to stand maturity

90 (Canullo et al., 2011). However, little is known about the effects of environmental conditions

91 driven by, e.g., elevation, slope aspect, stand maturity on taxonomic, functional and

92 phylogenetic diversity settings of beech forest understory vascular plants. In relation to climate,

93 we predict that plants at higher elevations (experiencing colder temperatures) would exhibit

94 lower taxonomic, functional and phylogenetic diversity than at lower elevations. This expectation

95 is based on the assumption that long-term harsher thermal conditions may select for a restricted

96 bunch of species and traits suited to cope with constraining thermal environments (Milla &

97 Reich, 2011; Spasojevic et al., 2014). Also, as functionally similar species tend to be closely

98 related (Webb et al., 2002), we expect high-elevation plots to be distinguished by lower

99 phylogenetic diversity than at lower elevations.

100   In relation to management, mature stands result from relative habitat stability which generally

101   generates a highly selective and competitive environment for light capture filtering for forest floor

102   species capable to persist under reduced light availability (Campetella et al., 2011; Lohbeck et

103   al., 2013; Landuyt et al., 2018). Persistence under closed canopy conditions should be

104   promoted by traits and resource strategies that should be shared across species (Campetella et

105   al., 2011; Lohbeck et al., 2013). As a result, mature stands of beech forests are generally

106   associated with reduced levels of species diversity and characterized by plants with similar

107   strategies to withstand limiting light conditions in the understory layer than younger, more

108   disturbed plots (Campetella et al. 2011; Scolastri et al. 2017; Landuyt et al., 2018). Therefore,

109   we anticipate closed canopy, mature stands to be characterized by lower values of plant

110   diversity (taxonomic, functional, phylogenetic) than younger plots. Furthermore, slope aspect

111   provides additional habitat heterogeneity and possibilities for ecological differentiation (e.g.,

112   Copeland & Harrison, 2015). For example, in rugged landscapes of the Northern Hemisphere,

113   mesic-related species tend to occur on north-facing slopes, whereas termophilous taxa prefer

114   south-facing slopes (Warren, 2008; Copeland & Harrison, 2015). However, multifaceted studies

115   have not specifically taken the role of aspect into account.

116   Here, we examined effects of elevation (macroclimatic factor), slope aspect (proxy for

117   microclimate) and stand maturity (management-related and microclimatic variable) on

118   taxonomic, functional and phylogenetic diversity in Northern Apennines beech forest

119   understories. With our multifaceted study we aim at i) offering a more comprehensive view of

120   plant diversity patterns, and ii) providing insights about effectiveness of the biodiversity

121   monitoring plan that is in place for the studied beech forests, that generally examined changes

122   in taxonomic diversity as the core indicator of forest conservation status (e.g., Chiarucci &

123   Bonini, 2005; Arévalo et al. 2012; Maccherini et al., 2018). We formulated three specific

124   questions: 1) Are high-elevation plots characterized by less species, trait convergence and

125   phylogenetic clustering, i.e., lower taxonomic, functional and phylogenetic diversity, than low-

126 elevation plots? 2) Do understory plants in less disturbed and more mature habitats show a

127 reduction in plant diversity (lower taxonomic, functional and phylogenetic diversity) when

128 compared with more disturbed forests? 3) Are taxonomic, functional and phylogenetic diversity

129 affected by slope aspect?

130

131 **2. Materials and methods**

132

133 *2.1. Study area, climate and management*

134

135   We studied vascular plants in the understory vegetation of two forested areas, namely Pistoia

136 (PIS) and Casentino (CAS), both located in Northern Apennines, Italy. These forests are

137 dominated by European beech (*F. sylvatica*) and correspond to two distinct mountainous

138 regions (Figure 1), located at different elevations between approximately 1000 and 1600 m a.s.l.

139 (Table 1). Casentino forests are found at lower elevations than Pistoia (Table 1). The main

140 geological substrate of both PIS and CAS is represented by sandstone, and the forests are

141 found on acidic brown soils, embedded in similar landscape mosaics. The forest plots (originally

142 20 for PIS and 22 for CAS) are part of a biodiversity monitoring plan of forests in Tuscany

143 (Forest Inventory of Tuscany; Chiarucci & Bonini, 2005; Arévalo et al., 2012). As a selection of

144 the original set, nineteen 20 m x 20 m plots were located using GPS and delimited – nine plots

145 in CAS and ten in PIS. This selection was operated aiming at collecting plots with comparable

146 characteristics both for edaphic conditions and land use. The same plots were surveyed twice

147 for floristics, in 2001 and 2009, always during late June and beginning of July, when most of the

148 species were in their phenological maximum (flowering and aboveground biomass production).

149 Plant species composition was recorded within each plot, as presence/absence data.

150   Traditionally, Apennines beech forests are logged for firewood and timber supply every 15-30

151 years (Campetella et al., 2016). Time since last disturbance event, hence stand maturity, is

152   considered a key management-related driver of diversity in the understory of these forests, with

153   lower species diversity found in older stands (Canullo et al., 2011; Campetella et al., 2016).

154   Basal area is effectively associated with stand maturity and stage of succession, as it shows

155   strongly positive correlation with stand age (Lebrija-Trejos & Bongers, 2008; Lebrija-Trejos et

156   al., 2010; Pinho et al., 2017), while being also affected by climatic and edaphic conditions. Yet,

157   in this case, we consider basal area as a reliable predictor for stand maturity. During the study

158   period 2001-2009, no logging occurred in the nineteen beech forest stands.

159

160   **Table 1** Average values and standard deviation (at plot scale) of environmental variables

161   related to macroclimate (elevation, MAP, MAT), microclimate (aspect, slope) and stand maturity

162   (basal area) in the two forested areas. Bold text identifies variables used as predictors (fixed

163   effects) in the model – see below.

	Elevation	MAP	MAT	**Aspect**	Slope	**Basal area**
	(m a.s.l.)	(mm y^{-1})	(°C)	(rad)	(°)	(m^2 ha^{-1})
Casentino (CAS)	1107 ± 145	1400 ± 69	6.5 ± 0.6	4.2 ± 1.7	37.8 ± 10.8	34.4 ± 8.9
Pistoia (PIS)	1503 ± 108	2166 ± 162	5.1 ± 2.5	4.1 ± 1.9	19.3 ± 9.1	40.9 ± 4.7

164

165   To define the environmental conditions of the forest stands, we collected six variables for

166   each plot (in 2001), namely elevation (m), mean annual precipitation (MAP; mm y^{-1}), mean

167   annual temperature (MAT; °C), aspect (rad), slope (°), and basal area (m^2 ha^{-1}) – Table 1. We

168   included here MAP and MAT to describe the climatic context of the study areas, but not for

169   statistical analyses as they were both spatially interpolated from weather stations (close to plots)

170   using elevation as predictor. Slope was also discarded from the analyses, as it was negatively

171   correlated with elevation (Pearson's correlation test: -0.68; p-value < 0.01).

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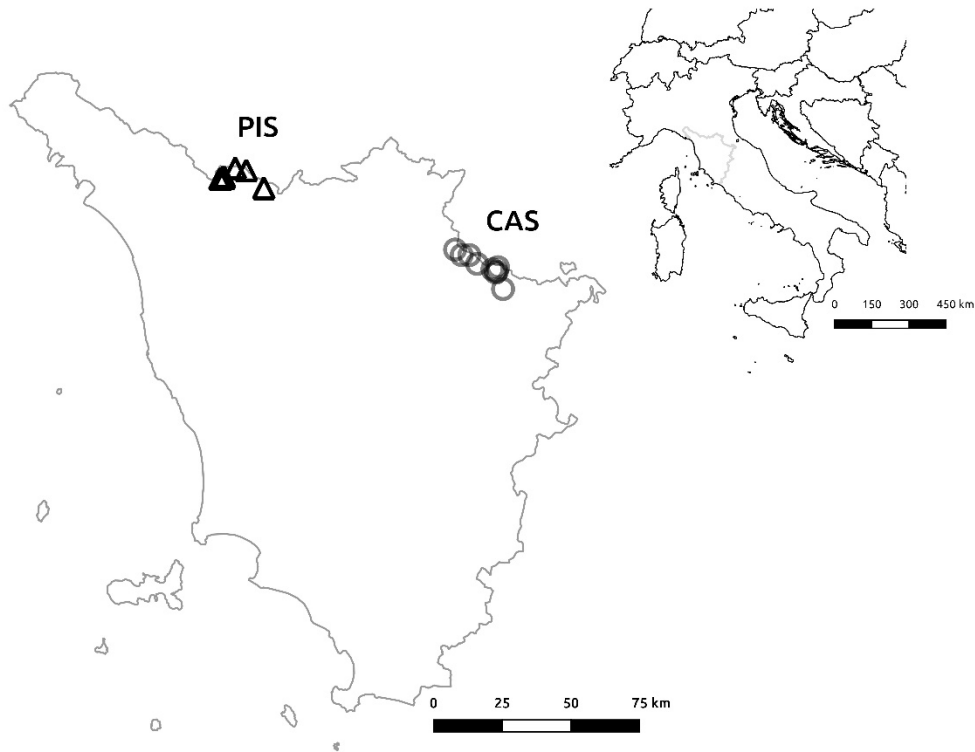
Figure 1. Location of the two study areas (Pistoia = PIS; triangles, and Casentino = CAS;

circles) in the Tuscany region, Central Italy.

2.2. Species, functional traits and phylogenetic data

We focused on vascular plant species occurring in the beech forest understory layer, and

across all plots the total species richness counted 130 species. Species nomenclature follows

Pignatti (1982). For plant functional traits, we gathered data from online databases, namely

CLO-PLA (Klimešova & de Bello, 2009), BiolFlor (Kühn et al., 2004), LEDA (Kleyer et al., 2008).

Specifically, we compiled fifteen traits, some of which were combined to groups to reflect a

certain dimension of plant ecological strategy (data coverage in percent of species given in

parentheses for each trait and trait group): 1) life form (100%); 2) plant lifespan (100%); 3)

reproduction type (89%); 4) flowering phenology (100%) – defined by onset (100%) and

186   timespan (100%) of flowering; 5) clonal traits (100%) – i.e., clonal ability (100%), clonal growth

187   organs (86%), lateral spread (88%); 6) storage organ type (89%); 7) plant height (100%); 8)

188   foliar traits (100%) – i.e., specific leaf area (73%), leaf dry matter content (72%), leaf mass

189   (70%), leaf size (70%), and leaf persistence (100%); see also Appendix I containing the

190   species-traits matrix. These traits or trait groups were used to calculate species pairwise

191   distances based on Gower distance, i.e., allowing for different variable types to be combined

192   and for missing values, and subsequently used for calculating community-level mean pairwise

193   distance (see below). We had trait data for at least 70% of species but more complete data for

194   most traits. The fact that some traits were combined to groups, together with the use of Gower

195   distance, further mitigated the potential effect of missing trait data. This is because within these

196   trait groups, at least one trait had complete data so that distances between all species pairs

197   could be calculated.

198   The used traits are informative on an array of different ecological functions (Weiher et al.,

199   1999; Ottaviani et al., 2017; Klimešová et al., 2018), that is, resource acquisition, retention, use

200   and competitive ability (i.e., plant height, foliar and clonal traits), reproduction (i.e., type,

201   flowering phenology, clonal traits), on-spot persistence (i.e., plant lifespan, storage organ type),

202   space occupancy (i.e., clonal traits), ability to resprouting after disturbance (i.e., life form,

203   storage organ type). For phylogeny, we consulted Daphne database (phylogenetic supertree for

204   Central European flora; Durka & Michalski, 2012) obtaining a phylogenetic tree for 112 of our

205   130 species which has been used for calculating cophenetic distances between pairs of

206   species. Species missing phylogenetic information were excluded from this analysis.

207   We calculated taxonomic (species richness), functional and phylogenetic diversity indices in

208   each plot for both the sampling years (2001 and 2009). We computed functional diversity (FD)

209   by using mean pairwise distances (Weiher et al., 1998) for each trait (or trait group), as well as

210   for all the traits combined (multiple-trait). Mean pairwise trait distances were calculated based

211   on Gower distance. For phylogenetic diversity (PD), we used the same index as per FD (i.e.,

212   mean pairwise distances), but based on cophenetic distances between pairs of species

213   stemming from the species phylogenetic tree (Webb et al., 2002).

214

215   *2.3.   Statistical analyses*

216

217   We performed linear mixed effect models (LMEs; Zuur et al., 2009) to examine the relations

218   between response variables (i.e., taxonomic, functional or phylogenetic diversity) and predictors

219   (i.e., elevation, aspect, basal area; not correlated among them; Appendix II). We ran eleven

220   LMEs, that is, one for each response variable, and each model included the three predictors

221   (set as fixed effects). From visual inspection, response variables did not exhibit issues related to

222   normality and homoscedasticity. In the models, we accounted both for repeated measures

223   across years (same plots visited twice, in 2001 and 2009 for floristics) and nested sampling

224   design (plots nested into two separate sites, CAS and PIS), by setting the identity of plots as a

225   random effect nested within sites (random intercept). In each model, we identified important

226   predictors for each diversity facet as variables showing marginally significant (p-values < 0.1) or

227   significant p-values ($p \leq 0.05$). We then quantified the variance explained by the fixed effects,

228   and fixed plus random terms in the LMEs (hereafter indicated as marginal and conditional R^2,

229   respectively; Nagakawa & Schielzeth, 2013). We also controlled for significant effects of two-

230   ways interaction terms among predictors on the response variables.

231   We ran Non-metric Multidimensional Scaling (NMDS) to ordinate plots in the two forested

232   areas (CAS and PIS) in both years (2001 and 2009) based on their species composition. NMDS

233   was performed on Bray-Curtis distances on untransformed cover data reducing the number of

234   dimensions to two, without step-across dissimilarities (because only a small fraction of plots (<

235   5%) did not share any species). The start configuration of the NMDS was defined by results of a

236   metric scaling ordination (i.e., principal coordinate analyses, PCoA). Then 50 iterations of

237   NMDS with random start configurations where run and compared to the start configuration by

238   means of Procrustes analysis. This resulted in a slightly lower stress value compared to the

239   start configuration (0.18) and was used to plot the samples in the ordination space. To test for

240   significant distinctiveness in species composition, we performed Analysis of Similarity (ANOSIM;

241   Bray-Curtis similarity measure; N of permutations = 999): i) between sites with years combined

242   (i.e., CAS *vs* PIS), and ii) across sites comparing years separately (i.e., CAS 2001 *vs* PIS 2001

243   and CAS 2009 *vs* PIS 2009). R-values close to 1 indicate highly dissimilar groups, while R-

244   values close to 0 identify highly similar groups (Clarke, 1993). We carried out all the analyses in

245   the statistical environment R (R Core Team, 2016), using the packages *picante* (Kembel et al.,

246   2010; calculation of FD and PD), *FD* (Laliberté & Legendre, 2010; Gower distance matrices of

247   traits), *ape* (Paradis et al., 2004; cophenetic distance matrix), *vegan* (Oksanen et al., 2017;

248   NMDS, ANOSIM), *nlme* (Pinheiro et al., 2016; LMEs) and *MuMIn* (Bartoń, 2018; marginal and

249   conditional R^2).

250

251   **3. Results**

252

253   Five significant relations between predictors and diversity indices resulted from LMEs (Table

254   2; Figure 2; models for all response variables, including insignificant relationships, are reported

255   in Appendix III). Elevation was significantly associated with changes in diversity for three

256   metrics: species richness, flowering phenology FD, and storage organ FD. Elevation had a

257   negative effect on species richness, that is, low-elevation plots (CAS) were species-richer than

258   high-elevation plots (PIS). Storage organ type FD also decreased with elevation, whereas

259   flowering phenology FD increased with elevation. Aspect did not predict any change in diversity

260   metrics, while basal area was negatively correlated with two diversity indices: foliar traits and

261   multiple traits FD (Table 2; Figure 2). Phylogenetic diversity did not show any significant

262   relationship with predictors. Two-way interaction terms between predictors did not affect any

263   diversity pattern.

264

265   **Table 2**. Summary statistics reporting the significant (p-value ≤ 0.05; in bold), or marginally

266   significant (p-value ≤ 0.1) relationships between environmental predictors and diversity facets.

267   Coefficient values, p-values, marginal R^2 (variance explained by fixed effects in the models, i.e.,

268   by predictors), conditional R^2 (variance explained by fixed plus random effects) are indicated.

269

Diversity facet	Predictor	Coefficient value	P-value	Marginal R^2 (%)	Conditional R^2 (%)
Taxonomic (SR)	Elevation	-0.008	**0.025**	33.0	71.8
Flowering phenology (FD)	Elevation	<0.001	**0.043**	14.2	22.6
Storage organs (FD)	Elevation	<-0.001	**0.033**	29.0	29.0
Foliar traits (FD)	Basal area	-0.003	0.072	15.0	76.6
Multiple-traits (FD)	Basal area	-0.002	**0.047**	13.6	35.2

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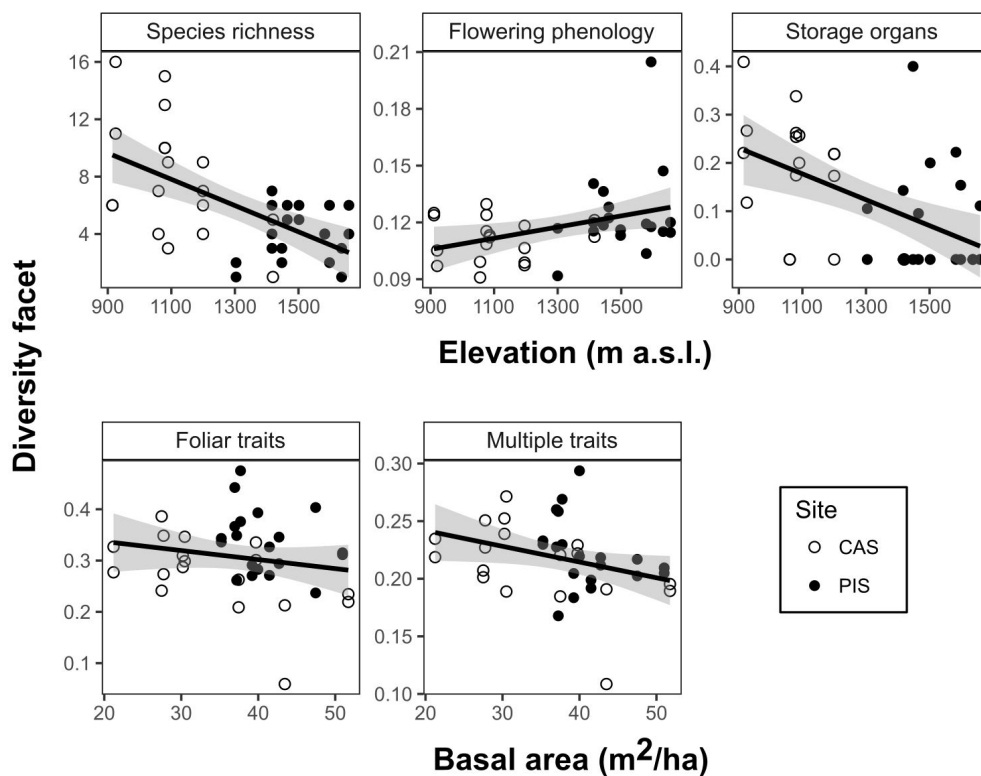
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272   **Figure 2.** Scatterplots with fitted regression lines reporting the significant relationships

273   between environmental predictors and diversity facets. Grey-shaded areas identify 95% CIs.

274

275   The ordination analysis (NMDS, stress = 0.179; Figure 3) revealed that beech forest

276   understory vegetation in CAS and PIS have different compositions, as confirmed by ANOSIM

277   between sites with years combined (R-value = 0.60; p-value = 0.001). In the ANOSIM that

278   compared years separately between sites, we found that while CAS and PIS remained

279   significantly different in their compositions in 2001 and 2009, they were becoming more similar

280   over time (CAS 2001 *vs* PIS 2001: R-value = 0.65; p-value = 0.001; CAS 2009 *vs* PIS 2009: R-

281   value = 0.51; p-value = 0.001).
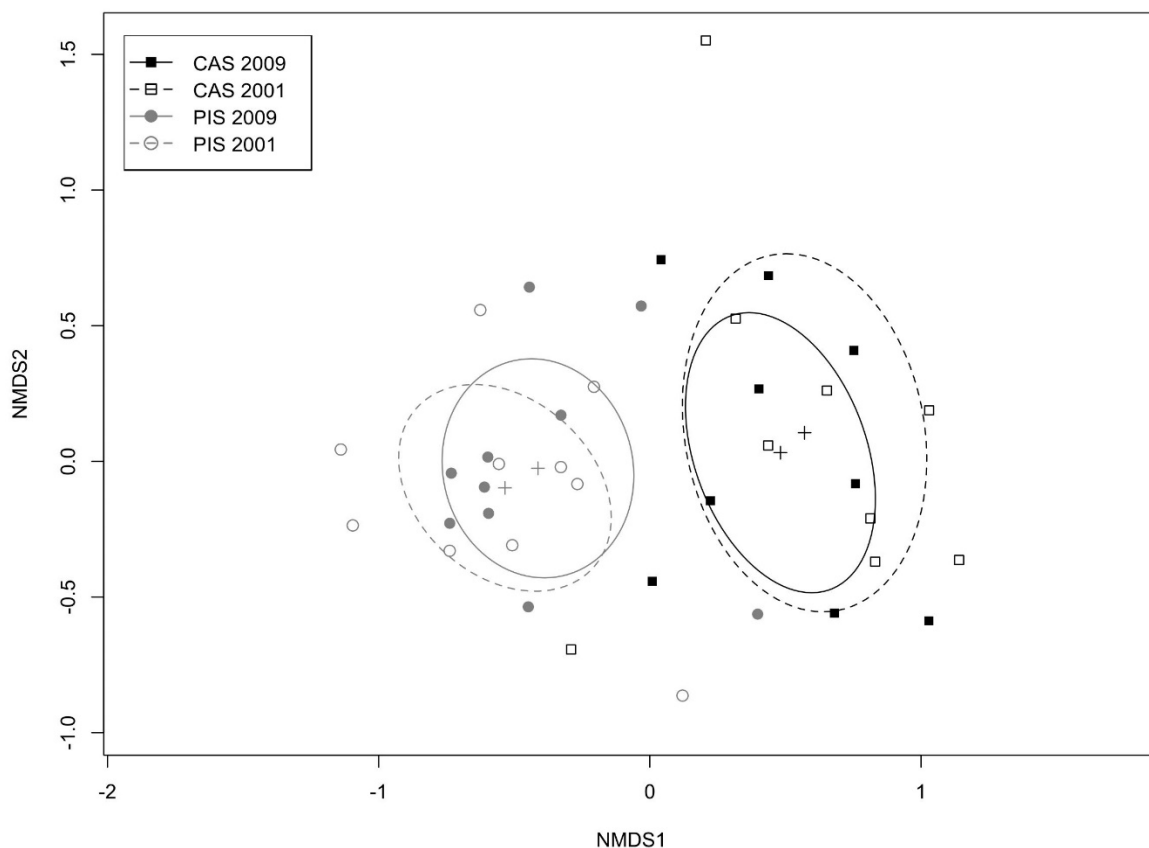
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283

284   **Figure 3.** Ordination of species compositions with ellipses representing one standard

285   deviation around the median of each of the four groups (CAS and PIS, 2001 and 2009).

286   Crosses represent ellipse centroids.

287

288   **4. Discussion**

289

290   The macroclimatic factor, elevation, operated as the main driver of diversity (Read et al.,

291   2014; Milla & Reich, 2011). Elevation (the most important predictor among the fixed effects in

292   the models) determined patterns of three diversity metrics, namely species richness and

293   functional diversity of two traits. Yet, stand maturity which we considered in the models through

294   basal area (Lebrija-Trejos et al., 2010; Pinho et al., 2017) played a significant role in driving FD

295   patterns of two traits. Aspect, a proxy for microclimate that can affect species and functional

296   composition of plant communities (Warren, 2008; Copeland & Harrison, 2015), did not predict

297   any diversity pattern in our case. This lack of influence may be caused by microclimatic effects

298   being overruled by variables related to macroclimate and management. Nevertheless, this

299   inference requires deeper scrutiny. The large amount of variance explained by fixed plus

300   random effects (conditional R^2), varied between 22.6% and 76.6% whereas the variance

301   explained by fixed terms only ranged between 13.6% and 33% (Table 2). This suggests that

302   other environmental parameters (e.g., resource availability, humidity, solar irradiance at the

303   forest floor; Lohbeck et al. 2013; Landuyt et al., 2018), processes (e.g., biotic interactions), and

304   likely edge-effect related to surrounding forest patches (Canullo et al., 2017) not considered in

305   this study may be important in shaping different facets of diversity. For storage organ FD, the

306   lack of difference between conditional and marginal R^2 would imply that diversity of this trait was

307   exclusively affected by the fixed effects, especially elevation. Unexpectedly, interactions among

308   predictors did not exert any significant effect on diversity patterns. This may be caused by

309   limitations related to small sample size. Phylogenetic diversity did not significantly vary in

14

310 relation to elevation, slope aspect and stand maturity. This lack of tangible change indicates that

311 phylogeny was not significantly affected by any of the environmental variables considered in this

312 study.

313

314 *4.1. Effects of elevation and stand maturity on multifaceted diversity patterns*

315

316 Focusing on specific relations between elevation and diversity facets, we have found partial

317 support to our hypothesis. Consistent with expectations, a lower number of species was found

318 at higher elevations. This finding, when combined with reduced FD values for storage organs at

319 high-elevation plots, suggests that limiting abiotic conditions may have selected for a reduced

320 number of specialized species sharing similar resource-storage strategies, and that may

321 promote cold tolerance at higher elevations (Milla & Reich, 2011; Read et al., 2014).

322 Conversely, more benign thermal conditions at lower elevations may facilitate the coexistence of

323 a greater number of species, functionally more diverse in resource-storage strategies than those

324 found at higher elevations (Spasojevic et al., 2014). Flowering phenology instead did not follow

325 the research predictions. On the one hand, increasing FD of flowering phenology with elevation

326 implies a functional differentiation for timing and length of flowering in the understories at higher

327 elevations (being onset and timespan of flowering forming this trait; see above, and Appendix I).

328 On the other hand, understory vegetation at low elevations converged functionally towards a

329 common, short blooming period. This may be advantageous for understory plants in the

330 deciduous beech forests at lower elevations experiencing longer growing seasons, hence more

331 extended canopy closure than at higher elevations. This may indicate that forest-floor plants can

332 avoid the light limitation caused by the canopy shading effect by anticipating and restricting their

333 flowering phenology in plots at lower elevations. Examples of these early-flowering, short-

334 blooming species belong to Ranunculaceae (e.g., *Anemone nemorosa* L., *Helleborus bocconei*

335 Ten., *Helleborus foetidus* L., *Hepatica nobilis* Mill.) and to Euphorbiaceae (e.g., *Mercurialis*

336   *perennis* L., *Euphorbia amygdaloides* L., *Euphorbia dulcis* L). In addition, climatic variations are

337   predicted to be particularly exacerbating in mountainous regions (Dobrowski & Parks, 2016;

338   Lamprecht et al., 2018). Intensifying climate fluctuations may also alter flowering phenology

339   (Godoy et al., 2009; Crimmins et al., 2010) which may facilitate the coexistence of species with

340   different flowering phenology. We can therefore cautiously infer that changing climate may have

341   contributed to determine shifts in flowering phenology of forest understories at higher elevations,

342   but we have no direct information on this aspect which should be better explored in future

343   studies.

344   Basal area, a reliable proxy for stand maturity and management regime (Lebrija-Trejos &

345   Bongers, 2008; Lebrija-Trejos et al., 2010; Pinho et al., 2017), showed a negative correlation

346   with functional diversity, a finding consistent with predictions. Increasing stand maturity is

347   reflected in greater basal area, and this exerted negative effects on multiple traits and foliar

348   traits FD. Light limitation under closed canopy, mature stands may have imposed strong

349   ecological constraints on beech forest understory plants (e.g., Campetella et al., 2011; Lohbeck

350   et al., 2013). This may have filtered for specialized understory biota sharing similar functional

351   strategies, mainly related to foliar traits and overall functional type (identified by all traits

352   combined, informing on an array of functions). Conversely, in young, open-canopy forests, FD

353   of understory vascular species increased thanks to more diverse and possibly more exploitative

354   strategies that may foster competitive ability for resource acquisition, such as light capture

355   (Canullo et al., 2011; Lohbeck et al., 2013).

356

357   *4.2. Spatial and temporal turnover of species composition*

358

359   The ordination analysis unraveled how forest understories in the two areas were

360   compositionally distinct, and this inference was confirmed by the ANOSIM test. Further, we

361   have found that the two areas were becoming compositionally more similar over the period

362   2001-2009, as highlighted by results from NMDS and ANOSIM comparing plots of the same

363   years between the two sites. We indeed found that in 2009 understory vegetation between CAS

364   and PIS were less distinct (i.e., lower R-value) than the 2001-plots, a trend that may potentially

365   progress with intensifying land-use and climate change (McKinney & Lockweed, 1999; Li &

366   Waller, 2015). Such trend to biotic homogenization is generally linked to a reduced group of

367   "winner" species tending to outcompete "loser" species under abruptly changing environmental

368   conditions (McKinney & Lockweed, 1999). Understanding the implications for ecology and

369   conservation associated with biotic homogenization is a challenging task, and would require

370   further attention. Lastly, we can carefully infer that regional species pool may have exerted an

371   effect on multifaceted diversity patterns (Zobel, 2016) as the two forested areas were

372   compositionally well distinct (even though this separation is decreasing over time). We

373   encourage future research to tackle this interesting biogeographic task by using larger datasets

374   that are better suited to study such macroecological issue.

375

376   **5. Conclusions: implications for conservation practices**

377

378   Our results, even if emerging from a limited dataset, emphasize the importance of

379   considering different diversity facets simultaneously (Cadotte & Tucker, 2018). Such a

380   multifaceted approach can promote a better understanding on relations between plant diversity

381   and environmental conditions – key information for improving effectiveness of conservation

382   efforts. Conservation planning and priorities may be defined based on which diversity facets are

383   of major ecological and biogeographic relevance. This is a context- and case-dependent matter,

384   always challenging to tackle. Different metrics can indeed display incongruent patterns, as in

385   this case, and may be difficult to be translated into conservation practices, but more informed

386   decisions can be taken using insights gathered from multifaceted studies (Cadotte & Tucker,

387   2018).

388   Regarding the performance of the specific biodiversity monitoring plan that is in place for the

389   Tuscany forests, this research provides a more comprehensive ecological understanding about

390   plant diversity-environment links. This information is key for refining the existing monitoring plan.

391   We suggest to systematically include functional diversity (and, on a cautionary ground, also

392   phylogenetic diversity because of the small sample size of this study) instead of relying only on

393   taxonomic metrics (e.g., Bonini & Chiarucci, 2005).

394

395   **Author contributions**

396

397   GO conceived the research idea; AC directed the project in which data were collected

398   (cooperation between University of Siena and LAMMA); GB coordinated the collection and

399   assembly of the floristic data; GO, LG and MM gathered the functional trait and phylogenetic

400   data; LG conducted the analyses; GO wrote the first version of the manuscript; all the co-

401   authors significantly contributed to revisions.

402

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417   **References**

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Appendix I. Table reporting the species x traits matrix for the 130 understory vascular plant species occurring in the 19 beech forest plots included in this study.

Species	Life form	Plant lifespan	Reproduction type		Flowering phenology		Clonal traits				Storage organ	Plant height	Foliar traits				
			Gen	Veg	Start	Timespan	Clonal ability	Main CGO	Lateral spread 1	Lateral spread 2			LM	SLA	LS	LDMC	LP
Adenostyles australis	H	P	NA	NA	6	2	1	NA	NA	NA	NA	0.8	NA	NA	NA	NA	0
Adiantum capillus-veneris	G	P	NA	NA	7	3	1	10	R	NA	R	0.4	NA	NA	NA	NA	0
Aegopodium podagraria	H	P	0	1	6	2	1	10	R	I	R	0.558	753.55	28.8	13500.23	230	0
Agrostis tenuis	H	P	0.5	0.5	6	2	1	10	R	I	R	0.25	10.17	34.43	335.67	259.67	0
Ajuga reptans	H	P	0.5	0.5	5	4	1	9	S	H	R	0.16	17.37	34.7	556	153	1
Alliaria petiolata	H	WA	1	0	4	3	1	15	O	L	TR	0.45	213.94	41.28	7514	161.3	1
Anemone nemorosa	G	P	0	1	3	3	1	10	R	I	R	0.14	123.87	27.6	3003	205	0
Aquilegia vulgaris	H	MLP	1	0	5	3	1	15	O	L	TR	0.55	142.01	26	9402	295	0
Arabis hirsuta	H	P	1	0	5	3	1	9	R	I	R	0.32	15.76	28.1	374	166	1
Aremonia agrimonoides	H	P	0.5	0.5	5	2	1	9	R	L	R	0.24	NA	NA	NA	NA	1
Asplenium adiantum nigrum	H	SLP	0.5	0.5	7	2	1	9	R	L	R	0.3	NA	NA	NA	NA	1
Asplenium trichomanes	H	P	0.5	0.5	7	2	1	9	R	L	R	0.175	95.5	10.9	1042	337	0
Athyrium filix-foemina	H	LLP	0.5	0.5	7	2	1	9	R	L	R	0.65	5603.01	12.1	67730	292	0
Avenella flexuosa	H	P	0.5	0.5	6	3	1	NA	O	NA	NA	0.07	2.92	17.41	40.56	329.55	1
Blechnum spicant	H	MLP	0.5	0.5	7	3	1	9	R	L	R	0.325	860.86	10.9	9350	266	1
Brachypodium rupestre	H	P	0.5	0.5	6	2	1	9	R	I	R	0.7	NA	NA	NA	NA	0
Brachypodium sylvaticum	H	P	0.5	0.5	7	2	1	9	R	L	R	0.825	20.43	44.34	3886.55	308.47	0
Bunium bulbocastanum	G	P	1	0	6	2	1	11	O	L	B	0.41	37.88	17.01	745	150.48	0
Campanula trachelium	H	P	0.5	0.5	7	2	1	9	R	L	R	0.6	92.25	39	3601	159	0
Cardamine bulbifera	G	P	0	1	5	2	1	10	R	I	R	0.4	52.89	40.41	2207	149.56	0
Cardamine chelidonia	T	A	NA	NA	6	2	0	NA	NA	NA	NA	0.4	NA	NA	NA	NA	0
Cardamine heptaphylla	G	P	NA	NA	4	3	1	10	R	I	R	0.37	700	38.38	28081.25	137.07	0
Cardamine impatiens	H	A	0.5	0.5	5	3	1	NA	NA	NA	TR	0.36	7.08	33.8	239	311	1
Carex digitata	H	P	1	0	5	1	1	9	R	L	R	0.1	15.65	30.31	480	274.15	1
Carex flacca	G	P	0	1	5	3	1	9	R	I	R	0.4	34.35	15.21	634.75	332.96	1
Carex sylvatica	H	P	0.5	0.5	6	2	1	9	R	L	R	0.42	29.75	30.9	677	324	1
Cephalanthera damasonium	G	P	0.5	0.5	5	2	1	10	R	L	R	0.35	55.27	30.63	1607.25	166.06	0
Cephalanthera longifolia	G	P	0.5	0.5	5	2	1	10	R	L	R	0.23	50.79	35.57	1770.34	185.12	0
Cephalanthera rubra	G	P	0.5	0.5	6	2	1	10	R	L	R	0.25	NA	NA	NA	NA	0
Circaea lutetiana	G	LLP	0.5	0.5	6	3	1	12	R	I	T	0.31	69.45	36.7	2643	193.5	0
Cirsium arvense	G	P	0.5	0.5	7	3	1	10	R	I	R	0.86	190.54	15.4	3857.5	141.66	0
Clinopodium vulgare	H	P	0.5	0.5	7	3	1	10	R	I	R	0.37	44.78	23.6	1055	258	0

Species																	
Crepis leontodontoides	H	P	NA	NA	4	7	0	NA	NA	NA	NA	0.4	NA	NA	NA	NA	0
Cruciata glabra	H	P	0.5	50	4	3	1	10	S	I	R	0.2	NA	NA	NA	NA	0
Dactylis glomerata	H	P	1	0	5	3	1	9	R	L	R	0.45	83.17	23.12	2303.67	262.5	0
Digitalis micrantha	H	P	NA	NA	5	3	0	NA	NA	NA	NA	0.9	NA	NA	NA	NA	0
Dryopteris affinis	H	MLP	0.5	0.5	7	3	1	9	R	L	R	1.3	2172.01	25.53	54489.25	233.55	1
Dryopteris filix-mas	H	P	0.5	0.5	7	3	1	9	R	L	R	0.75	3953.17	24.2	95617	295	0
Epilobium angustifolium	H	P	0.5	0.5	7	2	1	10	R	I	R	0.5	201.6	22.61	3811	228	0
Epilobium montanum	H	P	0.5	0.5	6	4	1	10	R	I	R	0.35	91.76	27.45	2187	229.33	0
Epipactis helleborine	G	SLP	0.5	0.5	6	3	1	10	R	L	R	0.6	95.03	29.04	2582.67	204.17	0
Epipactis microphylla	G	P	0.5	0.5	6	3	1	10	R	L	R	0.1	NA	NA	NA	NA	0
Euphorbia amygdaloides	C	P	0.5	0.5	4	2	1	15	O	L	TR	0.37	13.34	24.04	312.75	286.04	1
Euphorbia dulcis	G	P	0.5	0.5	5	1	1	10	R	I	R	0.3	12.26	33.27	420	238.54	0
Festuca altissima	H	P	1	0	6	2	1	9	R	L	R	0.75	62.7	29.15	2403.5	254.05	1
Festuca heterophylla	H	P	1	0	6	3	1	9	R	L	R	0.27	NA	NA	NA	NA	1
Festuca robustifolia	H	P	1	0	5	4	1	9	R	L	R	0.15	2.55	14.8	25.79	324.14	1
Fragaria vesca	H	P	0.5	0.5	5	2	1	9	R	H	R	0.11	132.86	23.17	2393.5	388	1
Galeopsis pubescens	T	A	1	0	7	3	0	NA	NA	NA	TR	0.35	8.34	63.81	NA	170.87	0
Galium album	H	P	0.5	0.5	6	4	1	10	R	I	R	0.87	2.9	23.42	58.5	162.37	0
Galium aparine	T	A	1	0	6	5	0	NA	NA	NA	TR	0.71	5.7	34.68	161.33	140	1
Galium odoratum	G	P	0.5	0.5	5	2	1	10	R	I	R	0.22	13.64	53.2	361	243	1
Galium rotundifolium	C	MLP	0.5	0.5	6	4	1	1	S	I	NA	0.15	1.95	45.96	110	140.34	0
Geranium columbinum	T	A	1	0	6	2	0	NA	NA	NA	TR	0.27	20.38	27.45	560.5	268	1
Geranium nodosum	H	P	0.5	0.5	5	3	1	10	R	NA	R	0.3	NA	NA	NA	NA	0
Geranium purpureum	T	SA	1	0	5	5	0	NA	NA	NA	TR	0.22	NA	NA	NA	NA	1
Geranium robertianum	T	SA	NA	NA	5	6	0	NA	NA	NA	TR	0.22	41.18	32.68	1224	185.7	1
Geranium sanguineum	H	P	0.5	0.5	6	3	1	10	R	I	R	0.22	57.24	21.83	1167	259	0
Gymnocarpium dryopteris	G	MLP	0.5	0.5	7	2	1	10	R	I	R	0.25	115.68	65.51	7176	175.95	0
Helleborus bocconei	G	P	NA	NA	2	3	1	10	R	NA	R	0.4	NA	NA	NA	NA	1
Helleborus foetidus	C	P	1	0	3	3	1	10	R	L	R	0.34	467.55	14.5	8718.08	180.71	1
Hepatica nobilis	H	MLP	0.5	0.5	3	2	1	9	R	L	R	0.1	108.17	27.16	2887.75	186.4	1
Hieracium sylvaticum	H	P	NA	NA	5	4	0	10	R	NA	R	0.5	NA	NA	NA	NA	0
Holcus lanatus	H	P	0.5	0.5	6	3	1	9	R	I	R	0.32	21.8	34.03	970.83	230.18	1
Hypericum montanum	H	SLP	0.5	0.5	6	3	1	14	S	I	TR	0.35	18.03	24.6	444	274	0
Hypericum perfoliatum	H	P	0.5	0.5	7	2	1	14	S	I	NA	0.7	NA	NA	NA	NA	0
Hypericum perforatum	H	P	0.5	0.5	7	2	1	14	S	I	TR	0.36	8.73	26.06	147.3	303	0
Koeleria macrantha	H	P	1	0	6	2	1	10	R	L	R	0.07	NA	11.81	454	327	0
Lamiastrum galeobdolon	H	P	NA	NA	5	4	1	NA	NA	NA	NA	0.39	68.19	25.35	1564	270	0

Lamium album	H	P	0.5	0.5	4	7	1	10	R	I	R	0.32	42.65	35.9	1970.51	170	1
Lathyrus latifolius	H	P	0.5	0.5	7	2	1	10	R	I	R	2	435.76	18.7	7017	220	0
Lathyrus venetus	G	P	NA	NA	4	2	1	10	R	L	R	0.5	NA	NA	NA	NA	0
Lathyrus vernus	G	P	0.5	0.5	4	2	1	10	R	L	R	0.25	132.09	39.64	4380	198.1	0
Lilium bulbiferum	G	P	0.5	0.5	6	2	1	13	O	L	B	0.6	26.79	18.43	461	140.52	0
Lilium martagon	G	P	1	0	6	2	1	13	O	L	B	0.47	162.39	25.58	4471	136	0
Luzula forsteri	H	P	0.5	0.5	4	2	1	9	R	L	R	0.15	NA	NA	NA	NA	0
Luzula luzulina	H	P	0.5	0.5	6	2	1	9	R	I	R	0.14	NA	NA	NA	NA	0
Luzula nivea	H	P	0.5	0.5	6	3	1	9	R	I	R	0.65	NA	NA	NA	NA	1
Lycopodium annotinum	C	P	0.5	0.5	8	2	1	1	S	H	NA	0.15	0.23	25	5.8	363.64	1
Melica uniflora	H	P	0.5	0.5	5	2	1	9	R	I	R	0.32	NA	39.6	NA	NA	0
Melittis melissophyllum	H	P	0.5	0.5	5	2	1	10	R	L	R	0.3	45.22	53.5	2586.75	148.29	0
Mercurialis perennis	G	P	0.5	0.5	4	2	1	10	R	I	R	0.21	83.87	25.68	1890.5	224.5	0
Milium effusum	H	P	0.5	0.5	5	3	1	10	R	I	R	0.62	28.94	33.35	1621.5	251	1
Moehringia trinervia	T	A	1	0	5	3	1	14	O	L	TR	0.17	2.39	36.1	81.33	179.33	0
Mycelis muralis	H	P	1	0	7	2	1	9	R	L	R	0.5	NA	NA	NA	NA	1
Myosotis arvensis	T	A	1	0	4	6	1	5	O	NA	NA	0.23	28.22	29.38	759.5	123	1
Myosotis sylvatica	H	P	0.5	0.5	5	3	1	NA	R	NA	R	0.22	19.72	29.68	613.33	146	1
Orchis maculata	G	P	1	0	5	4	1	16	O	L	TR	0.7	54.2	23.8	1391	119.77	0
Oxalis acetosella	G	P	0.5	0.5	4	2	1	9	R	I	R	0.09	7.69	63.39	806	129.79	1
Phyteuma orbiculare	H	P	1	0	6	4	1	14	O	L	TR	0.29	NA	36.1	NA	NA	0
Phyteuma scorzonerifolium	H	P	NA	NA	6	3	0	NA	NA	NA	NA	0.9	NA	NA	NA	NA	0
Poa nemoralis	H	P	0.5	0.5	6	2	1	9	R	I	R	0.5	8.86	49.9	536.5	323.5	0
Polygonatum multiflorum	G	P	0.5	0.5	5	2	1	10	R	I	R	0.44	48.35	43.84	2038.25	148.21	0
Polypodium vulgare	C	P	0.5	0.5	8	2	1	9	R	I	R	0.3	525.33	12.35	6246	289	1
Polystichum aculeatum	G	P	1	0	8	2	1	9	R	L	R	0.8	2439.34	13.97	40709.58	299.06	1
Polystichum lonchitis	H	P	1	0	7	3	1	9	R	L	R	0.3	1092.98	7.37	8352.22	307.8	1
Polystichum setiferum	G	P	1	0	8	2	1	9	R	L	R	0.8	NA	19.75	NA	NA	0
Potentilla micrantha	H	P	0.5	0.5	3	3	1	9	R	L	R	0.07	NA	NA	NA	NA	1
Prenanthes purpurea	H	P	0.5	0.5	7	2	1	10	R	L	R	0.87	43.2	65.86	2945.25	123.72	0
Primula vulgaris	H	P	0.5	0.5	2	4	1	9	R	L	R	0.12	224.4	28.6	2187.75	154	1
Pteridium aquilinum	G	P	0.5	0.5	7	3	1	10	R	H	R	0.97	NA	18.44	NA	298	0
Ranunculus lanuginosus	H	P	0.5	0.5	5	3	1	9	R	L	R	0.43	236.14	NA	5917.37	153.62	0
Ruscus hypoglossum	C	P	NA	NA	12	5	1	NA	NA	NA	NA	0.6	NA	NA	NA	NA	0
Salvia glutinosa	H	P	1	0	7	4	1	14	O	L	TR	0.47	213.42	53.62	11482.75	102.89	0
Sanguisorba minor	H	P	1	0	5	4	1	9	R	L	R	0.2	159.72	20.5	3124.25	311.1	1
Sanicula europaea	H	P	0.5	0.5	5	2	1	9	R	L	R	0.27	70.91	30.95	2414	198	1

Species	1	2	3		4		5				6	7	8				
Saxifraga rotundifolia	H	P	0.5	0.5	6	4	1	9	R	L	R	0.25	NA	NA	NA	NA	1
Scrophularia scopolii	H	P	0.5	0.5	6	4	1	10	R	L	R	1.2	NA	NA	NA	NA	0
Sedum cepaea	T	A	1	0	6	2	0	NA	NA	NA	TR	0.13	1.37	21.81	30.33	53.04	1
Senecio fuchsii	H	P	0.5	0.5	8	2	1	10	R	I	R	1.5	NA	NA	NA	NA	0
Silene dioica	H	P	0.5	0.5	4	6	1	10	R	I	R	0.56	73.28	36.78	3533	112	1
Silene viridiflora	H	P	NA	NA	6	3	0	NA	NA	NA	NA	1	NA	NA	NA	NA	0
Solidago virgaurea	H	P	0.5	0.5	7	4	1	9	R	L	R	0.5	94.49	21.68	2302.5	227	0
Stellaria media	T	A	1	0	1	12	1	1	S	L	TR	0.16	8.74	53.68	488	84	1
Stellaria nemorum	H	P	0.5	0.5	5	5	1	1	S	I	R	0.32	37.44	45.06	1613	145.91	1
Tamus communis	G	P	1	0	5	2	1	15	O	L	TR	2.25	220.04	30.3	6124	151	0
Teucrium chamaedrys	C	P	0.5	0.5	7	2	1	10	R	H	R	0.13	7.59	15.68	134	305.71	1
Teucrium scorodonia	C	P	0.5	0.5	7	3	1	10	R	I	R	0.27	87.47	17.78	939	378.5	1
Thymus pulegioides	C	P	1	0	6	5	1	14	O	I	TR	0.18	NA	24.7	NA	NA	1
Trifolium medium	H	P	0.5	0.5	6	3	1	10	R	I	R	0.4	65.74	20.61	1437	263	0
Trifolium ochroleucum	H	P	1	0	6	2	1	14	R	L	TR	0.5	NA	NA	NA	NA	0
Urtica dioica	H	P	0.5	0.5	7	4	1	10	R	H	R	0.87	101.22	28.48	3842	212.5	0
Vaccinium myrtillus	C	P	0	1	4	5	1	10	R	I	R	0.31	4.04	20.46	77.65	331.83	0
Veronica chamaedrys	C	P	0.5	0.5	5	3	1	10	R	I	R	0.23	15.8	31.59	355.5	270.46	1
Veronica officinalis	C	P	0.5	0.5	6	3	1	9	R	I	R	0.14	10.47	NA	54	280	1
Veronica urticifolia	C	P	0.5	0.5	6	3	1	10	R	I	R	0.4	NA	NA	NA	NA	0
Vicia ochroleuca	H	P	NA	NA	5	2	0	NA	NA	NA	NA	0.6	NA	NA	NA	NA	0
Viola alba	H	P	0	1	3	2	1	9	R	I	R	0.07	NA	NA	NA	262	1
Viola biflora	H	P	0.5	0.5	5	4	1	9	R	I	R	0.11	2.88	52.12	140.25	134.1	1
Viola reichenbachiana	H	P	0.5	0.5	3	3	1	9	R	L	R	0.11	17.56	30	488	225.69	1

Abbreviations, units and variable types of plant functional traits

1) Raunkiaer life form (P = phanerophyte, NP = nano-phanaerophyte, H = hemicryptophyte, Ch = chamaphyte, G = geophyte, T = therophyte). Nominal
2) Plant lifespan (A = annual, SA = summer annual, WA = winter annual, P = Perennial, SLP = short lived perennial <5 years, MLP = medium lived perennial 5-50 years, LLP = long lived perennial >50 years). Nominal
3) Reproduction type (Gen = predominantly generative, Veg = predominantly vegetative). Fuzzy
4) Flowering phenology: Start of flowering (number of month), Timespan of flowering (number of months). Ordinal
5) Clonal traits: Clonal ability (1 = presence, 0 = absence), Main clonal growth organ (CGO, refer to CLOPLA3 for classification of the 17 organ types), Lateral spread 1, Runners (S = Stolon, R = Rhyzome, O = Other), Lateral spread 2, Distance per year (L = low if <0.01m/year, I = intermediate if 0.01-0.25 m/year, H = high if >0.25 m/year). Combination of different variable types: Nominal, Binary, Ordinal
6) Storage organs (B = bulb, T = tuber, R = rhyzome, TR = tap root). Nominal
7) Plant height (m). Continuous
8) Foliar traits: LM = leaf mass (mg), SLA = specific leaf area (mm^2 mg^{-1}), LS = leaf size (mm^2), LDMC = leaf dry matter content (mg g^{-1}), LP = leaf persistence (1 = presence = evergreen, 0 = absence = deciduous). Combination of different variable types: Continuous, Binary

NA = not available or missing data

1 **Appendix II**: Coefficient of correlation (Pearson's test) among the three environmental

2 predictors (* = p-value ≤ 0.05).

3

	Elevation	Basal area	Aspect
Elevation	1		
Basal area	0.54*	1	
Aspect	-0.11	-0.22	1

4

5

Appendix III. Overview of significant fixed effects of the linear mixed effects models for each diversity facet, in which random effects accounted for repeated measures of each plot (i.e., in two different years, 2001 and 2009) and clustering of the plots in the two sites (PIS and CAS). Marginal and conditional R^2 describe the explained variance by the fixed, and by the fixed and random effects together, respectively.

Species richness

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	-0.01	0.003	14	-2.52	**0.0247**
Aspect	-0.10	0.364	14	-0.29	0.7784
Basal area	-0.06	0.100	14	-0.59	0.5674
Marginal R^2 (%)	0.33				
Conditional R^2 (%)	0.72				

Foliar traits FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	-0.74	0.4722
Aspect	0.00	0.006	14	0.54	0.6002
Basal area	0.00	0.002	14	-1.95	**0.0717**
Marginal R^2 (%)	0.15				
Conditional R^2 (%)	0.77				

Flowering phenology FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	2.22	**0.0432**
Aspect	0.00	0.002	14	0.40	0.6961
Basal area	0.00	0.000	14	-0.59	0.5628
Marginal R^2 (%)	0.14				
Conditional R^2 (%)	0.23				

Canopy height FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	1.01	0.3299
Aspect	0.00	0.000	14	-0.01	0.9899
Basal area	0.00	0.000	14	-0.79	0.4432
Marginal R^2 (%)	0.12				
Conditional R^2 (%)	0.19				

Clonal traits FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	1.69	0.1130
Aspect	0.00	0.008	14	0.64	0.5309
Basal area	0.00	0.002	14	-1.61	0.1302
Marginal R^2 (%)	0.11				
Conditional R^2 (%)	0.20				

Reproduction type FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	-1.70	0.1106
Aspect	0.00	0.005	14	0.04	0.9718
Basal area	0.00	0.001	14	-1.04	0.3172
Marginal R^2 (%)	0.19				
Conditional R^2 (%)	0.19				

Storage organ type FD

	Coefficient value	Standard error	DF	t-value	P-value

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	-2.37	**0.0329**
Aspect	0.00	0.011	14	-0.28	0.7810
Basal area	0.00	0.003	14	-0.82	0.4250
Marginal R^2 (%)	0.29				
Conditional R^2 (%)	0.29				

Life form FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	1.02	0.3234
Aspect	0.00	0.008	14	0.16	0.8731
Basal area	0.00	0.002	14	0.35	0.7280
Marginal R^2 (%)	0.06				
Conditional R^2 (%)	0.06				

Plant lifespan FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	-0.96	0.3542
Aspect	0.01	0.015	14	0.76	0.4570
Basal area	0.00	0.004	14	-0.56	0.5839
Marginal R^2 (%)	0.12				
Conditional R^2 (%)	0.78				

Multiple traits FD

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.00	0.000	14	0.51	0.6177
Aspect	0.00	0.003	14	0.32	0.7544
Basal area	0.00	0.001	14	-2.18	**0.0470**
Marginal R^2 (%)	0.14				
Conditional R^2 (%)	0.35				

Phylogenetic diversity

	Coefficient value	Standard error	DF	t-value	P-value
Elevation	0.09	0.107	14	0.81	0.4330
Aspect	4.08	8.305	14	0.49	0.6307
Basal area	0.25	2.274	14	0.11	0.9150
Marginal R2 (%)	0.04				
Conditional R2 (%)	0.54				